Evolution of Life Histories in Birds

Reproductive Strategies and Survival – Relationship with Ecology, Social System and Life Histories

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To my grandfathers who would
have liked to be among us to see
this accomplishment…

General Contents

Contents per chapter

Summary

Understanding the diversity in life-history traits that influence fitness is a central goal in evolutionary biology. Survival and reproductive strategies vary considerably between species as well as within species and populations. Despite growing understanding of such diversities in the last decades, much remains to be learnt. Trade-offs between life-history traits may explain the variation in survival and reproductive strategies. Additionally, both ecological and social factors may influence the cost-benefit balance associated with survival and reproductive strategies, and thus influence their evolution. Nevertheless, studies investigating the relative roles of life history, ecology, and social system remain scarce. In this dissertation, I try to fill in this gap in our understanding of life history evolution, using birds as model systems.

In the first part of this dissertation, I focused on behavioural traits related to reproductive strategies and their diversity among species. In **Chapter 1**, I investigate the age at first reproduction relatively to the age of physiological maturity and its effect on fitness, using a comparative approach. My findings show that lifespan explains most of the variation in the mean age at first reproduction among species, where long lifespans associate with late reproductive onsets. Moreover, most species had higher fitness when delaying the onset of reproduction beyond the age of maturity. An optimally delayed onset of reproduction correlated with a long mean lifespan and a large body size. The decrease in lifetime reproductive success and future survival linked to early age at first reproduction may reflect costs of reproduction for inexperienced individuals. These results empirically support the hypothesis that the pace of life and cost of reproduction fundamentally affect reproductive timing.

In **Chapter 2**, I investigate the variation among species in parental care responses to diverging predation risks. Specifically, I study experimentally how species adjust the trade-off between survival and reproduction. To do so, in species with different attributes and current brood value (e.g. higher brood value when the nest vulnerability, re-nesting potential or survival expectancy are low), parents feeding their nestlings were exposed to models and vocalizations of a common predator of nestlings and of adults. Across species, parents reduced their visitation rate only in the presence of a predator dangerous to adults, adding to the growing evidence that birds adjust their reproductive strategies depending on the type of predator in ecological time. Species with a short lifespan, a low chance of re-nesting before the end of the breeding season, or open nests reduced their visitation rate more than long-lived species, with high re-nesting potential, or nests in cavities. The role of within season re-nesting potential for the evolution of parental care responses to risk was previously demonstrated in a study that assessed parental responses during the incubation period to an increased risk to their offspring among species. **Chapter 2** further supports the role of within season re-nesting potential in parenting decisions during the nestling period when parents are at risk. Taken together, these results suggest that within season and lifetime re-nesting potential are major drivers of parental care strategy among species.

In the second part of this dissertation, I focused on the variation in age-specific survival both inter- and intra-specifically. In **Chapter 3**, I investigate the variation in first-year survival, maximum longevity and their relationship, using a comparative approach. A slow life-history pace (large body size, long incubation and nestling period, low reproductive investment) are associated with high juvenile survival and with long lifespan but, longevity and first-year survival were also correlated with environments implying diverging predation risks. While species breeding in open nests on the ground, thus exposed to high nest predation risk, have higher first-year survival, terrestrial species living in dense habitat, thus higher adult predation risk, have a shorter lifespan. First-year survival and maximum longevity are positively correlated, as predicted by the classical evolutionary theory of ageing. However, most species significantly deviate from the regression

between first-year survival and maximum longevity, having either (i) unexpectedly high first-year survival/long lifespan or low first-year survival/short lifespan, or (ii), unexpectedly high first-year survival/short lifespan or low first-year survival/long lifespan (i.e. combinations fully contrasting with the theory of a positive relationship). Different ecological, life-history and social factors are associated with the different types of deviations. For example, a high first-year survival associated with short lifespan is predominantly observed in species that live in stable environments, breed cooperatively, have precocial young, or a specialized diet, while the reverse was partly true for species with a low first-year survival but a long lifespan. Together with other studies, these findings underpin the importance of considering age-specific survival in evolutionary studies and provide novel insights into life-history evolution.

In **Chapter 4**, I explore survivals in the Siberian Jay (*Perisoreus infaustus*), using radio-tracking data. In this family-group-living bird species, predation is the primary cause of mortality, confirming the essential role of predation as a source of extrinsic mortality in birds. First year juveniles had substantially lower survival than older individuals and, among breeders, males had lower survival than females. While non-breeders have a lower survival in managed habitats with little visual cover and when having a low feather quality, both of these factors do not influence the survival of older individuals. Thus, these findings support that experience can buffer extrinsic mortality risk. Additionally, based upon previous research demonstrating that juvenile Siberian jays acquire critical anti-predator skills from experienced group members, they highlight that group living may provide social opportunities to learn critical life-skills. A lower juvenile survival in managed habitats may explain the accelerated population declines of many species living in such habitats. Hence, this finding could have useful implications for conservation management of endangered species.

Overall, the results presented in this dissertation reveal that age at first reproduction, parental decisions during nestling provisioning, and age-specific survival vary greatly within and among avian species. They demonstrate that the variation in reproductive strategies among species is principally explained by differences in long- and short-term reproductive prospects, and the cost of reproduction. Social and most ecological factors have only a low explanatory power for variation in reproductive strategies. However, this dissertation reveals that the social and ecological factors account for most of the variation in survival both within and among species, and that survival of different age classes are related to diverging social and ecological factors as well as life-history pace. Ultimately, this dissertation contributes to a better understanding of life-history evolution with possible implications for conservation biology.

Zusammenfassung

Das zentrale Ziel der Evolutionsbiologie ist das Verstehen der *life-history traits (*d.h. Lebenszyklusmerkmale). Überlebens- und Fortpflanzungsstrategien haben einen grossen Einfluss auf die Fitness, und unterscheiden sich zwischen und innerhalb von Arten sowie Populationen. Obwohl das Verständnis für diese Vielfalt in den letzten Jahrzehnten stark zugenommen hat, bleibt noch einiges zu lernen. Die Vielfalt und Variation von Überlebens- und Fortpflanzungsstrategien lässt sich durch *trade-offs* zwischen verschiedenen *life-history traits* erklären. Darüber hinaus beeinflussen ökologische und soziale Faktoren das Kosten-Nutzen Gleichgewicht, welche mit Überlebens- und Fortpflanzungsstrategien assoziiert sind, und beeinflussen so auch deren Evolution. Studien, die den Einfluss der *life-history*, der Ökologie und des sozialen Systems untersuchen sind selten. In dieser Dissertation versuche ich anhand von Vogelstudien zum Verständnis über die *life-history* Evolution beizutragen.

Im ersten Teil der Dissertation fokussiere ich mich auf Verhaltensmerkmale, die mit der Fortpflanzungsstrategie und der Diversität zwischen Arten zusammenhängen. In **Kapitel 1** untersuchte ich mit Hilfe einer vergleichenden Studie das Alter bei der ersten Fortpflanzung relativ zum Alter der physiologischen Reife und den Effekt auf die Fitness. Meine Ergebnisse zeigen, dass die Lebenserwartung die größte Abweichung des Durchschnittsalters bei der ersten Fortpflanzung erklärt, wobei eine hohe Lebenserwartung mit einem späten ersten Fortpflanzungszeitpunkt zusammenhängt. Zudem ist die Fitness bei den meisten Arten höher, wenn die erste Fortpflanzung nach dem Erreichen des Reifealters erfolgte. Eine optimal verzögerte erste Fortpflanzung korreliert mit einer langen Lebenserwartung und großer Körpergröße. Individuen, welche sich so früh wie möglich fortpflanzen, sind unerfahren und haben deshalb einen verminderten Fortpflanzungserfolg und geringere Überlebenschancen. Diese empirischen Daten unterstützen die Hypothese, dass die Lebenserwartung und der Fortpflanzungsaufwand den ersten Fortpflanzungszeitpunkt bestimmen.

In **Kapitel 2** untersuchte ich die zwischenartlichen Unterschiede in der Brutpflege unter erhöhtem Prädationsrisiko. In einer experimentellen Studie untersuchte ich, wie verschiedenen Arten den *trade-off* zwischen Überleben und Reproduktion ausgleichen. Die Studie untersuchte, wie sich das Fütterungsverhalten von Eltern in verschiedenen Arten verändert, wenn die Eltern oder Nestlinge Fressfeinden ausgesetzt wurden. Eltern aller Arten reduzierten die Nestbesuchsrate, wenn sie einem Fressfeind ausgesetzt wurden. Arten mit einer kurzen Lebenserwartung und einer niedrigen Wahrscheinlichkeit für eine Zweit- oder Ersatzbrut, sowie Arten, die in offenen Nestern brüten, reduzierten die Besucherfrequenz stärker als Höhlenbrüter oder Arten mit einer höheren Lebenserwartung und einer größeren Wahrscheinlichkeit für Zweit- oder Ersatzbruten. **Kapitel 2** betont die Wichtigkeit von Zweit- oder Ersatzbruten auf Entscheide während der Brutperiode, wenn Eltern selbst in Gefahr sind. Diese Resultate zeigen, dass die Lebensspanne und der Brutwert einen wichtigen Einfluss auf die Evolution der Brutpflegestrategien haben.

Im zweiten Teil der Dissertation fokussiere ich mich auf die altersspezifischen Schwankungen des Überlebens, innerhalb von Arten und zwischen Arten. In **Kapitel 3** untersuchte ich mittels einer vergleichenden Studie die Unterschiede im Überleben während des ersten Lebensjahres, die maximale Lebensdauer und deren Beziehung zueinander. Eine große Körpergröße, lange Brutzeit und Wachstumsperiode der Küken und eine niedrige Reproduktionsrate stehen mit einer hohen Überlebenswahrscheinlichkeit der Jungtiere und einer langen Lebenserwartung in Zusammenhang. Arten, die einem hohen Nestprädationsrisiko ausgesetzt sind, haben eine hohe Überlebenswahrscheinlichkeit während des ersten Lebensjahres, während bei bodenlebenden Arten die Altvögel einem höheren Risiko von Fressfeinden ausgesetzt sind und somit eine kürzere Lebenserwartung aufweisen. Die Lebensdauer und das Überleben im ersten Jahr sind positiv

korreliert, jedoch weichen die meisten Arten signifikant von der Regression zwischen dem Überleben im ersten Jahr und der maximalen Lebensdauer ab, weil sie (i) ein unerwartet hohes Überleben im ersten Jahr beziehungsweise lange Lebenserwartung aufweisen oder ein niedriges Überleben im ersten Jahr beziehungsweise eine kurze Lebenserwartung aufweisen oder (ii) ein unerwartet hohes Überleben im ersten Jahr beziehungsweise eine kurze Lebenserwartung oder ein niedriges Überleben im ersten Jahr beziehungsweise eine lange Lebenserwartung aufweisen. Unterschiedliche ökologische, *life-history* und soziale Faktoren stehen mit diesen verschiedenen Abweichungen in Zusammenhang. Zum Beispiel, eine hohe Überlebensrate im ersten Jahr, aber eine kurze Lebensdauer kommt oft bei Arten vor, die in stabilen Umgebungen leben, kooperativ brüten, Nestflüchter sind oder eine spezialisierte Ernährung haben. Die Erkenntnisse dieser Studie zeigen, dass das altersspezifische Überleben neue Einsichten in die Evolution der *life-history* ermöglicht.

In **Kapitel 4** untersuchte ich das Überleben von Unglückshähern (*Perisoreus infaustus*). Unglückshäher leben in Familiengruppen und die Haupttodesursache sind Fressfeinde. Jungvögel bis zum ersten Jahr haben eine geringere Überlebenschance als ältere Individuen. Innerhalb der Brüter haben Männchen eine geringere Überlebenschance als Weibchen. Jungvögel haben eine geringere Überlebenschance, wenn sie in bewirtschafteten Wäldern leben, welche wenig Sichtschutz bieten oder wenn sie eine schlechte Federnqualität aufweisen. Diese Ergebnisse zeigen, dass Erfahrung das Mortalitätsrisiko vermindern kann. Vor kurzem veröffentlichte Studien haben gezeigt, dass junge Unglückshäher von ihren älteren Artgenossen lernen, Fressfeinde zu erkennen, und betonen, dass das Leben in Gruppen soziale Vorteile für das Erlernen wichtiger Fertigkeiten mit sich bringt. Eine tiefere Überlebenswahrscheinlichkeit bei Jungvögeln in bewirtschafteten Lebensräumen könnte die Erklärung für die Populationsabnahme vieler Arten in bewirtschafteten Lebensräumen sein. Diese Resultate könnten wichtige Hinweise liefern im Bezug auf bedrohte Arten und für den Naturschutz von Bedeutung sein.

Die Resultate dieser Dissertation zeigen, dass das Alter bei der ersten Fortpflanzung, elterliche Entscheide während der Fütterungsperiode und altersabhängige Überlebenswahrscheinlichkeiten sich innerhalb und zwischen Vogelarten unterscheiden. Sie zeigen, dass die Unterschiede in den Reproduktionsstrategien der verschiedenen Vogelarten hauptsächlich damit erklärt werden können, ob es sich um eine kurz- oder eine langfristige Fortpflanzungsinvestition handelt und wie hoch die Reproduktionskosten sind. Soziale und ökologische Faktoren spielen dabei eine geringere Rolle. Die Erkenntnisse dieser Dissertation zeigen auch, dass soziale und ökologische Faktoren für die Schwankungen der Überlebenschancen innerhalb und zwischen Arten verantwortlich sind und dass das Überleben verschiedener Altersklassen mit den verschiedenen sozialen und ökologischen Faktoren sowie den Lebensspannen in Zusammenhang stehen.

General Introduction

"Evolution is the ultimate field-guide to biodiversity"
(Morris & Lundberg 2011)

A. Evolutionary and life-history theory

Making sense of the diversity of living organisms and their lifestyles has always been a goal of biologists. Darwin's theory of evolution by natural selection (Darwin 1859) provided the conceptual framework to understand this diversity. From then onward, science made great progress in this field since referred to as evolutionary biology. The theory of evolution is based on Darwin's assertion "survival of the fittest", wherein fitness is the ability of an organism to contribute offspring to the next generation (the evolutionary currency of their parents). The concept of fitness is crucial to explain the diversity of life: without differences in fitness, natural selection cannot act and adaptation does not occur (Losos *et al.* 2014). Therefore, understanding the variation in traits that influence fitness is critical and is the scope of life-history evolution (Roff 1992; Stearns 1992).

Life histories represent a particular category of adaptations as they apply to the actual currency of fitness (Losos *et al.* 2014). An individual's life history is the composite of all the variables that improve its match with its environment and contribute to the way it propagates itself. Life histories include size at birth, growth rate, age and size at physiological maturity, onset and magnitude of reproduction, parental care, mortality rate and lifespan (Reznick 2014). Another remarkable feature of life histories is their important diversity (Roff 1992; Stearns 1992). They can vary among related species as well as between individuals and populations within species. For example, some organisms reproduce as soon as they reach maturity, while others delay their onset of reproduction well beyond the age of sexual maturity. Some organisms produce many thousands of small offspring, while others produce just one or a few larger offspring. Some

organisms live only a few weeks while others live for decades, even centuries. Some organisms show prolonged parental care after giving birth while others show none. Variation in life histories provides the raw material for natural selection and thus, is a focus of evolutionary theory. Despite a growing understanding of the diversity in life histories, there is still much to be learned (Roff 1992; Robinson *et al.* 2010; Losos *et al.* 2014).

The concept of "trade-off" is a central feature to understand the intra- and inter-specific diversity in life histories (Stearns 1989). Without trade-offs, natural selection would favour immortal organisms that commence breeding at birth and produce an infinite number of good quality offspring, also known as "Darwinian demons". However, in reality individuals have a finite quantity of resource which must be competitively allocated to various functions, such as growth, reproduction, survival, and maintenance. Therefore, individuals are constrained in the way to distribute their resources and maximize their fitness (Lack 1947; Williams 1966; Stearns 1989). Trade-offs connecting life-history traits can constrain their simultaneous evolution, and are therefore fundamental to the understanding of the evolution of life histories (Roff 1992; Stearns 1992). Classical life-history trade-offs include the trade-off between reproduction and survival or current vs. future reproduction, known as "costs of reproduction" (Williams 1966; Reznick 1985), and the trade-off between number versus size of offspring (Smith & Fretwell 1974). Despite the importance of trade-offs for life-history theory, these trade-offs have been difficult to document (Roff & Fairbairn 2007).

B. Variation in reproductive strategies and survival

Reproductive strategies and survival are two major components of fitness and show considerable intra- and interspecific variation (Roff 1992; Stearns 1992). In this dissertation, I specifically address the variation in age at first reproduction, parental care, as well as juvenile and adult survival.

B.1 VARIATION IN REPRODUCTIVE STRATEGIES

B.1.1 Age at first reproduction

A critical reproductive "decision" in the life of an organism is when to start the breeding career (Figure A). Within species, the age at first reproduction varies. For instance, Weddell seals (*Leptonychotes weddellii*) may begin the reproductive career anywhere from 4 to 14 years (Hadley *et al.* 2006), while Wandering Albatrosses (*Diomedea exulans*) may begin reproduction from 6 to 20 years (Mourocq *et al.* 2016). Across species, age at first reproduction can range from a few months to 20 years in birds (Mourocq *et al.* 2016), and from a few weeks to 15 years in both fish (Wootton 2012) and mammals (Harvey & Zammuto 1985). Differences in individuals' quality or allocation strategies (Forslund & Pärt 1995; Fay *et al.* 2016) can explain this variation within species, while different species-specific and environmental characteristics among species can explain interspecific variation. Age at first reproduction influences the number of lifetime reproductive events and length of generation time, making it an important component of fitness and intrinsic growth rate of a population (Cole 1954; Caswell 1982). While well investigated within species, the relationship between the age at first reproduction and fitness remains equivocal across species (**Chapter 1**; Figure 1-3).

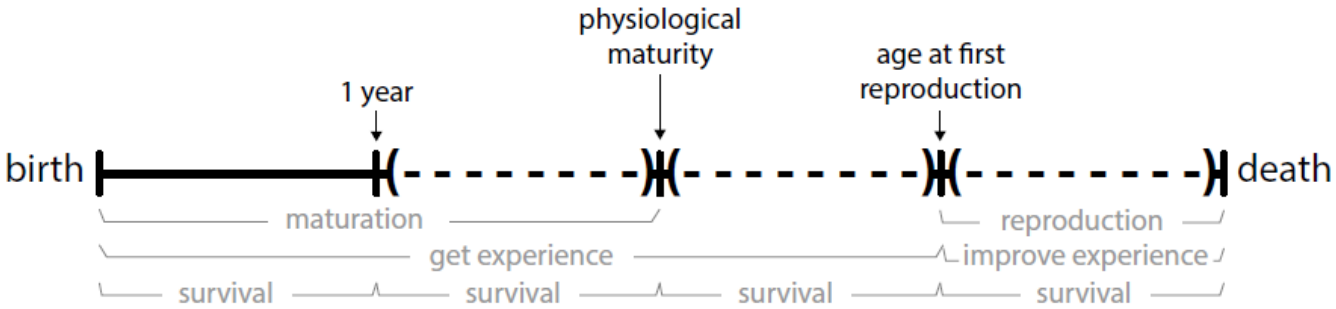

Figure A: Simplified schema of the life of an organism. The dashed line within parenthesis reflects the variation in the timing between the different events that can exist between individuals or species.

If no costs are associated with early onset of reproduction, organisms should start reproducing immediately upon reaching sexual maturity, thereby increasing the chance of surviving to reproductive age, and also increasing the number of lifetime reproductive events (Pianka & Parker 1975; Roff 1992; Stearns 1992; Charlesworth 1994). For example, this strategy is observed in many mice or shrews, and in most small passerines. However, many organisms delay the onset of reproduction beyond the age of sexual maturity. Thus, early reproduction may be costly either in terms of future survival or fecundity (Lack 1968; Roff 1992; Stearns 1992). Alternatively, it may be beneficial to delay breeding by enhancing experience (Curio 1983), or if the delay increases the chance to breed in a high quality territory, or with a high quality mate (Zack & Stutchbury 1992; van de Pol *et al.* 2007). For example, a delayed onset of reproduction is the rule in elephants and sea birds. The fact that in many species individuals do not initiate breeding, even though capable of doing so, still poses a challenge to biologists.

B.1.2 Parental care

Fitness is not only influenced by the onset of reproduction and the total quantity of reproduction, but also by parental care (Losos *et al.* 2014). The role of parental care on fitness has been highlighted by both theoretical and empirical studies (Royle, Smiseth & Kölliker 2012; Klug & Bonsall 2014). Parental care encompasses any behaviour parents provide to the offspring including, e.g., preparation of nests and burrows, care of young inside or outside the parent's body, food provisioning, and protection from harsh environment (predators, conspecifics, infections). Most birds and mammals provide parental care, whereas it is rare in fishes and invertebrates (Royle, Smiseth & Kölliker 2012). Different species, individuals, sexes, or even an individual throughout the breeding period, may differ in the nature or intensity of the care provided (Cockburn 2006; Klug & Bonsall 2010; Royle, Smiseth & Kölliker 2012; Caro *et al.* 2016). In altricial birds and mammals, care after birth (feeding, brooding, defense…) is extensive and

young are totally dependent for their survival on parental care, while nearly no parental care is provided in precocial species.

Parental investment should be influenced by the needs of the offspring and the capacity of the parents to provide care, as well as the cost-benefit balance of parental care (Klug & Bonsall 2010; Royle, Smiseth & Kölliker 2012). Obvious benefits are the improvement of growth rates, quality, and survival of the offspring, and hence ultimately an increase in the inclusive fitness of parents (Alonso-Alvarez & Velando 2012; Klug & Bonsall 2014). The costs may come from increased conspicuousness or risk-taking by the caring parents and a reduction in the time available for feeding (Sabat 1994; Alonso-Alvarez & Velando 2012). Because parental care is energetically costly, it can also reduce body condition and makes parents more susceptible to predation, disease or starvation, and reduce the potential for future reproduction (Alonso-Alvarez & Velando 2012). Theory predicts that the optimal amount to invest into parental care should be when benefits are maximised (Royle, Smiseth & Kölliker 2012).

An understanding of the evolution of parental care is of central importance in evolutionary biology. The investigation of the variation in risk-taking behaviour among species is a particularly good indicator of parental care strategies (Ghalambor & Martin 2000). Although a large number of studies focussed on parental care responses to risks concerning offspring, factors influencing these parental decisions are not yet well understood (Ibáñez-Álamo *et al.* 2015). On the contrary, studies of parental care responses to a risk affecting their own survival are valuable for understanding parental trade-off, as parents need to balance their risks of death against reproductive effort, however, such studies remain rare (Dale, Gustavsen & Slagsvold 1996; Hua *et al.* 2014).

B.2 VARIATION IN SURVIVAL

The survival of an organism is a crucial life-history trait that influences its fitness (Clutton-Brock 1988; Roff 1992; Grant & Grant 2000; Kjellander *et al.* 2004). Survival can vary among the stages

of life and differently influence the evolution of life-history traits (Figure A, section C1) and population dynamics (Promislow & Harvey 1990; Reznick, Bryga & Endler 1990; Clark & Martin 2007; Martin 2015). Hence, understanding variability in juvenile and adult survival is fundamental to life-history theory and conservation biology (Stearns 1976; Eberhardt 1985).

Longevity is commonly used as a proxy of adult survival and varies substantially within and among species. For instance, longevity in insects can range from 2 days in mayflies to 30 years in termite queens, in mammals from 2 years in mice to 200 years in whales, and in birds from 2 years in a rail to 60 years in albatrosses (Carey & Tuljapurkar 2003). A long life might allow for an increased number of reproductive events and a better adjustment to the environment (Griesser *et al.* in press). Hence, under the above conditions, natural selection should select for the evolution of increased lifespan. However, in environments where the risk of dying is high, short lifespan associated with an increased early reproductive investment should be favoured. This pattern is supported by both theoretical and empirical studies that demonstrate that the level of extrinsic mortality is the principal driver in the evolution of longevity (Williams 1957; Kirkwood 2002; Ricklefs 2010; but see: Dowling 2012).

Juvenile survival is a critical fitness parameter that may play an integral role in the evolution of life-history strategies. Studies on birds and mammals revealed that first-year survival is tightly linked with population growth rate (mammals: Sinclair 1996; birds: Clark & Martin 2007). In species with slow life-history pace, younger age classes represent up to half of the total population and account for a large contribution to the total reproductive value and demographic stochasticity (Sæther *et al.* 2013). In contrast to longevity (Carey & Tuljapurkar 2003; Hulbert *et al.* 2007; Healy *et al.* 2014), little attention is given to survival early on in life (Clark & Martin 2007; Robinson *et al.* 2010; Tarwater *et al.* 2011; Cox *et al.* 2014a). The reason lies in the difficulty to assess survival at this stage, but filed studies show that juvenile survival is highly variable within and among species. For instance, in the Tawny owl (*Stix aluco*) juvenile survival rate ranged from

0.07 to 0.33 (Millon *et al.* 2011), and from 0.86 to 0.17 among species of large herbivores (Gaillard *et al.* 2000).

Generally, adults have a higher and less variable survival than juvenile, and the two measure tend to be positively correlated (Caughley 1966; Charnov 1986; Sullivan 1989; Gaillard *et al.* 2000), but deviations occur (Abrams 1993; Chen & Maklakov 2012; Shokhirev & Johnson 2014). For instance, guppies subjected to lower juvenile survival due to higher level of predation exhibit longer lifespan (Reznick *et al.* 2004). Yet, there is little consensus about the drivers of such unusual survival patterns.

C. Role of life histories, ecology, and social system

Identifying the conditions and parameters that are associated with variation in reproductive strategies and survival, as well as their trade-off may help to understand their evolution (Roff 1992; Stearns 1992). Ecology, social factors, and life histories differ between individuals and among species. Independently or in combination, they can influence the cost-benefit balance associated with survival and reproductive strategies. In turn, differences in ecology, social factors, and/or life histories may explain plasticity in reproductive strategies and survival (Figure B). Most studies considered the role of ecology and life histories. Yet, studies that assess the relative role of life histories, ecology, and social system remain rare. In this section, I introduce how each of these parameters may influence reproductive strategies and survival.

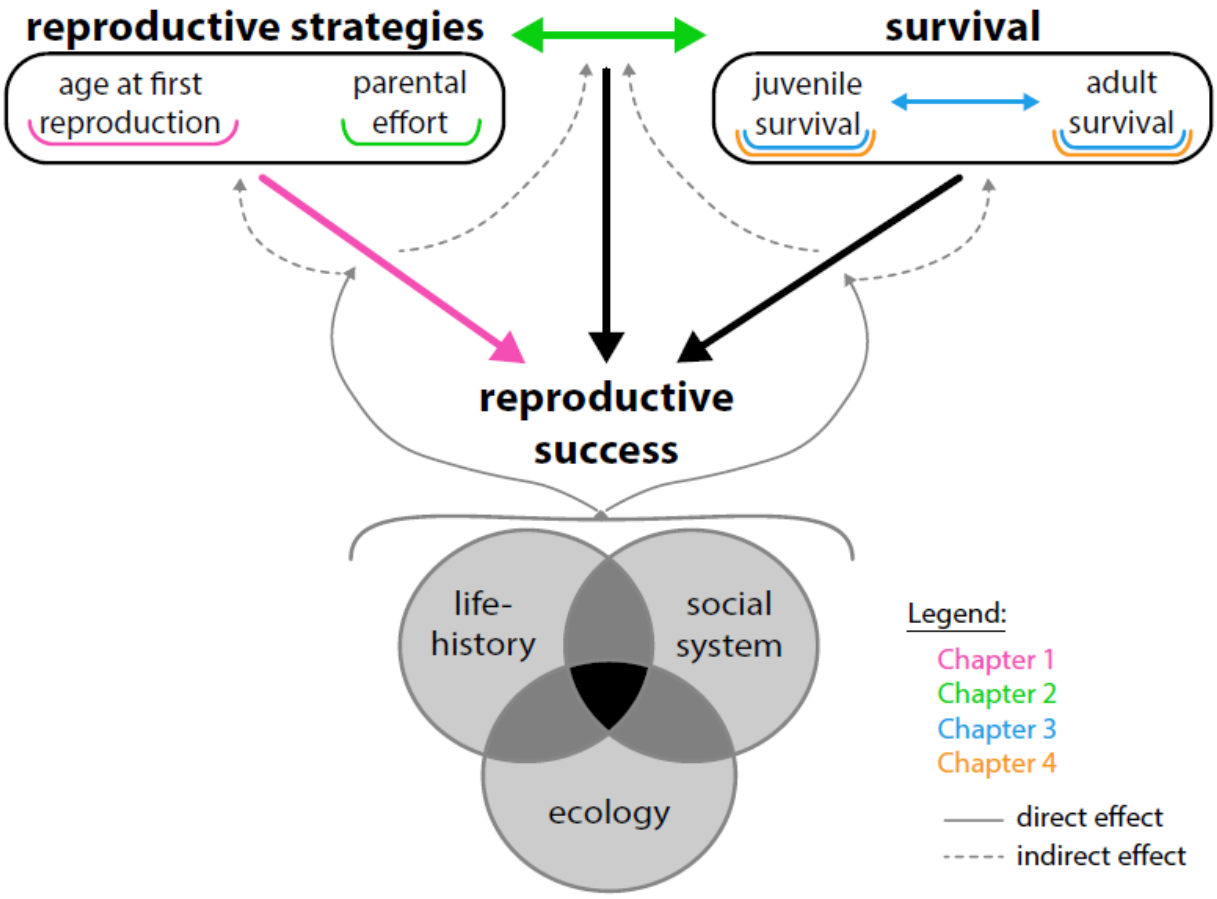

Figure B: Conceptual framework of the dissertation. Social system, ecology, life-histories, or any combination of these should influence the costs-benefits balance associated with survival and reproductive strategies, and thus may explain their variation within and among species. The aim of the dissertation was to identify the main drivers of the diversity of survival and reproductive strategies. See Appendix A to know which predictors have been investigated among each chapter.

C.1 LIFE-HISTORIES

Since resources are limited, all organisms face trade-offs in allocating their resources to the various components of the life history. Consequently, the way one life-history trait evolves is well correlated with the way other life-history components evolve (Reznick 2014) (see section A). Both body size and longevity correlate with life-history traits in many animals (Barbraud *et al.* 1999; Sibly & Brown 2007), and link to the slow-fast continuum in animal life-histories (Promislow & Harvey 1990; Martin 2002). In addition, theory and a growing number of empirical studies suggest that age-specific survival is particularly important to explain the slow–fast axis of life-history

variation (Michod 1979; Martin 2002; Kraus *et al.* 2005). This interplay of adult and offspring survival on the expression of life-history traits, however, has received insufficient attention (Ibáñez-Álamo *et al.* 2015).

Survival and longevity are often thought to be inversely related to reproductive effort (Stearns 1976; Stearns 1980). Increased fecundity or parental investment may reduce longevity, as time and resources that could be allocated to adult maintenance and avoidance of predation are instead devoted to offspring (Roff 1992; Stearns 1992). Current reproductive investment can also reduce the energy available for future reproduction (Roff 1992; Stearns 1992), and thus, a high reproductive investment in early life may lower survival probability (Clutton-Brock 1984; Viallefont, Cooke & Lebreton 1995).

Occurrence and intensity of fitness costs of reproduction vary among species according to their position on the fast–slow continuum of life history (Hamel *et al.* 2010). For instance, the trade-off between early investment and survival should be particularly important in long-lived species for which residual reproductive value in early life is high. Indeed, in species with high life expectancy, early mortality is especially costly as lifetime reproductive success varies primarily with reproductive lifespan (Reid et al. 2003). Inversely, in species with a fast life-history pace, costs from a reduction in offspring survival should be higher than a reduction in adult survival due to their low life-expectancy (Roff 1992; Stearns 1992). These differences in costs associated with the reproduction-survival trade-off among species from the fast or slow end of the life-history continuum, may explain that in birds and mammals, species with low prospects of adult survival generally initiate reproduction as soon as physiologically mature whereas species with low mortality rates may postpone first breeding beyond maturity (Harvey & Zammuto 1985; Ricklefs 2000a). It may also explain that species with a fast life-history pace favour parental care over their own survival whereas species with a slow life-history pace favour their own survival over parental care under harsh conditions (Ghalambor & Martin 2000; Ghalambor & Martin 2001).

C.2 ECOLOGY

Ecological characteristics such as habitat openness, geographical location, time of activity, or their diet, can influence the level and predictability of the acquisition of resource and the risk of predation, which may affect age-specific survival and the cost of early reproduction and parental care (Roff 1992; Stearns 1992). The skills required to survive and reproduce successfully may differ among ecological conditions and explain variation in survival and reproductive strategies (Nevoux, Weimerskirch & Barbraud 2007). For instance, in large herbivores the variation in survival differs among tropical, temperate, and arctic environments. This variation is generally higher in juveniles than adults. Also, different ecological conditions affect the survival among life stages (Gaillard *et al.* 2000). In birds, adult (Lloyd *et al.* 2014) and juvenile survival vary among latitude (Lloyd & Martin 2016).

Individual condition is expected to influence survival and their ability to invest into reproduction (Webb *et al.* 2002; Sadler 2012; Fay *et al.* 2016). Low or unpredictable access to food may impair immune-capacity, increase the risk of infections, and thus, reduce the capacity to escape from predators or deal with parasites (Alonso-Alvarez & Velando 2012). Therefore, a reduction in survival or reproductive investment is expected under low or unpredictable food resources (Martin 1987; Morrison & Hero 2003; Jones 2011; Ruffino *et al.* 2014; Caro *et al.* 2016). In birds and mammals, parents may desert their offspring (Clutton-Brock 1991; Szekely & Cuthill 1999) or initiate reproduction at a later age when food is in short supply (Vincenzi *et al.* 2013; Gilmore & Cook 2015). Finally, a recent study showed that birds evolved different life-history strategies to cope with environmental variability in food supply (Ruffino *et al.* 2014).

Stochastic predation is an important driver of the evolution of lifespan (Valcu *et al.* 2014). However, a recent study revealed that the effect of extrinsic predation pressures on longevity depends on the energy-allocation conditions. High extrinsic predation pressure favours a longer

lifespan when the cost of reproduction is high and resources are not limiting, while a shorter lifespan when reproduction is not costly and resources are scarce (Shokhirev & Johnson 2014). Predation risk constitutes a reproductive cost for breeding animal by imposing a "survival cost" through adult predation and a "fecundity cost" through offspring predation. This makes predation risk an important driver of reproductive strategies (Magnhagen 1991; Sih 1994). For instance, under increased predation risk, animals forgo reproduction (Ylönen 1989), reduce the number of offspring produced (Zanette *et al.* 2011), or reduce parental care (Gallagher *et al.* 2016). Having different fitness consequences, the risk of predation on offspring or adult should influence animals' reproductive strategies via distinct mechanisms (Lima & Dill 1990b; Magnhagen 1991; Dale, Gustavsen & Slagsvold 1996). However, studies testing the effect of adult and offspring predation risk on animal reproductive strategies simultaneously are scarce.

C.3 SOCIAL SYSTEM

The social system of species varies from solitarily, to ephemeral groups of unrelated individuals and family livings (Drobniak *et al.* 2015). Moreover, species can breed solitarily, in a pair or cooperatively (i.e., when individuals help raise conspecific offspring that are not their own: Griesser & Suzuki 2016b). These different social factors (unrelated and related to breeding) may influence age-specific survival and the cost of early reproduction and parental care. Yet, in comparative studies investigating the evolution of life histories, the role of social system received little consideration.

C.3.1 Social factor unrelated to breeding

In group-living species juvenile and adult survival is improved by risk dilution (Hamilton 1971), confusion effect (Miller 1922), enhanced predator detection (Bertram 1978), and increased foraging efficiency by reduction in individual vigilance (Pulliam 1973), but may also decrease through an enhanced competition (Brouwer *et al.* 2006). In insects, sociality influences longevity

where e.g., eusocial species live longer (Keller & Genoud 1997), and longevity associates with group formation in birds (Arnold & Owens 1998; but see: Møller 2006; Downing, Cornwallis & Griffin 2015; but see: Griesser *et al.* in press).

C.3.2 Social factor related to breeding

In cooperative breeding species, the presence of helpers may improve the survival of the breeder(s) through a reduction of parental effort (Khan & Walters 2002), and of the offspring via allo-feeding and enhanced protection against predator and parasites (Boland 1998; Valencia *et al.* 2006b; Pacheco *et al.* 2008; Lloyd *et al.* 2009; Van de Loock *et al.* 2017). In turn, the effect of helpers on survival or reproductive failure can influence breeders' investment strategies (Valencia *et al.* 2006a; Taborsky, Skubic & Bruintjes 2007; Lloyd *et al.* 2009). This may also depends on the ecological (Hatchwell 1999; Ebensperger *et al.* 2014), or social conditions (Silk 2007; Brouwer, van de Pol & Cockburn 2014). For instance, the survival of red-cockaded woodpeckers (*Leuconotopicus borealis*) breeders was enhanced of 21 to 42% in the presence of helpers, and breeders reduced incubation and nestling feeding (Khan & Walters 2002). In the red-winged fairy-wrens (*Malurus elegans*), provisioning rates were reduced in response to an increasing number of male, but not of female helpers (Brouwer, van de Pol & Cockburn 2014).

Species with a prolonged association with the parents beyond independency or post-fledging parental care (as in family-living species: Drobniak *et al.* 2015), may have higher first-year survival, either due to direct effects of parents on offspring, or to indirect effects from living in the family territory (Griesser, Nystrand & Ekman 2006a; Gruebler & Naef-Daenzer 2010; Weegman *et al.* 2016). Additionally, post-fledging parental care may allow compensation for offspring conditions (Shizuka & Lyon 2013). Thus, reproductive strategies (prior to fledging) could differ between species with and without post-fledging care.

Living surrounded by other individuals provides the opportunity for social learning (Griffin 2004; Seppänen & Forsman 2007). It may improve the ability and rapidity to develop critical skills

such as food acquisition and antipredator behaviours, which in turn may enhance survival and influence reproduction especially in variable environment (Griffin 2004; Hoppitt *et al.* 2008; Griesser & Suzuki 2017). For instance, in white-winged choughs (*Corcorax melanorhamphos*) the number of helpers correlates positively with the acquisition of foraging skill by juveniles and their prospect of surviving the first year (Heinsohn 1991).

D. Intra- and interspecific studies

The variation in life-history traits can be investigated within and between species, providing different insights into the diversity of life-history traits and can complement one another. Analyses at the species level allow assessing the ultimate sources of the variability in life-history traits, while intraspecific analyses give insights into the proximate factors responsible for this variability. Intraspecific studies allow us to identify factors beyond those revealed by interspecific studies such as their underlying mechanisms and functional significance. Moreover, useful generalisation can be made from comparative study, and intraspecific studies can be used to test or confirm the predictions derived from interspecific comparisons.

Generally, it is difficult to generalize findings from single species study because of differences in environmental context (social or ecological) and life-history attributes between species. However, intraspecific studies can be particularly useful, for instance, for defining efficient conservation management plans for endangered populations (Fryxell, Sinclair & Caughley 2014). Clearly, comparative studies provide only insight into correlations between factors. However, when phylogenetic relationships are taken into account, comparative studies can provide useful insight into the causes of variation and may highlight potential evolutionary influences (Harvey & Pagel 1991). More empirical comparative studies that account for phylogeny are needed to improve our understanding of life-history evolution.

- Chapter 1 -

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Lifespan and reproductive cost explain interspecific variation in the optimal onset of reproduction

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Abstract

Fitness can be profoundly influenced by the age at first reproduction (AFR), but to date the AFR-fitness relationship only has been investigated intraspecifically. Here we investigated the relationship between AFR and average lifetime reproductive success (LRS) across 34 bird species. We assessed differences in the deviation of the Optimal AFR (i.e., the species-specific AFR associated with the highest LRS) from the age at sexual maturity, considering potential effects of life-history as well as social and ecological factors. Most individuals adopted the species-specific Optimal AFR and both the mean and Optimal AFR of species correlated positively with lifespan. Interspecific deviations of the Optimal AFR were associated with indices reflecting a change in LRS or survival as a function of AFR: a delayed AFR was beneficial in species where early AFR was associated with a decrease in subsequent survival or reproductive output. Overall, our results suggest that a delayed onset of reproduction beyond maturity is an optimal strategy explained by a long lifespan and costs of early reproduction. By providing the first empirical confirmations of key predictions of life-history theory across species, this study contributes to a better understanding of life-history evolution.

Key Words: Age at first reproduction, comparative method, cost of reproduction, family formation theory, life-history theory.

1.1 Introduction

Life-history theory predicts that the timing of reproductive events during an individual's life affects its fitness (Cole 1954; Caswell 1982). An early age at first reproduction (hereafter AFR) can increase the number of lifetime reproductive events and shorten generation time, which, in a stable or growing population, should be favored by natural selection (Cole 1954; Bell 1980; Roff 1992; Charlesworth 1994). However, an early AFR may also be costly and reduce future survival or reproductive investment (Lack 1968; Roff 1992; Stearns 1992). Additionally, individuals could benefit from deferring breeding beyond sexual maturity if this enhances parenting skills ('constraint hypothesis': Curio 1983), secures access to higher quality territories or mates ('queuing hypothesis': Zack & Stutchbury 1992; van de Pol *et al.* 2007), increases reproductive output with age ('restraint hypothesis': Williams 1966; Forslund & Pärt 1995) or decreases reproductive senescence ('senescence hypothesis': Charmantier *et al.* 2006). If AFR is shaped by natural selection, then individuals should adopt the AFR that is associated with the highest fitness return, which may depend on individual quality and annual variation in environmental conditions.

Individuals of some species express no variation in AFR, while there is a large range in AFR in other species. In the latter case, only certain AFRs are associated with a high lifetime reproductive success (hereafter LRS), but the exact association appears to vary among species (Clutton-Brock 1988; Newton 1989; Oli, Hepp & Kennamer 2002; Krüger 2005; Charmantier *et al.* 2006; Millon, Petty & Lambin 2010; Kim *et al.* 2011; Tettamanti, Witvliet & Bize 2012; Zhang *et al.* 2015). Moreover, the relationship between the species-specific AFR that is associated with the highest LRS (hereafter termed Optimal AFR) and age of sexual maturity can vary across species (Komdeur 1996; Pyle *et al.* 1997; Oli, Hepp & Kennamer 2002; Krüger 2005). Yet, the reasons underlying this among-species variation remain unclear as we currently lack comparative studies that investigate the evolution of AFR and deviation in the timing of Optimal AFR during

reproductive lifespan across species. Such a study could contribute to our understanding of the general patterns of variation in this crucial life history trait.

Whether species-specific Optimal AFR either approximates or is shifted beyond the age of sexual maturity of the species may depend on interspecific variation in life-history or ecological factors. Across species, the pace of life (i.e. slow or fast life history) is likely to be a major factor influencing variation in AFR and timing of the species-specific Optimal AFR relative to the age of sexual maturity (Roff 1992; Stearns 1992; Charlesworth 1994). A short lifespan should be associated with little or no variation in AFR, and with an Optimal AFR that is close to the species' age of maturity, as any postponement would increase the risk of death before reproduction. In contrast, a long lifespan allows for a larger range in AFR and increases the likelihood of a delayed Optimal AFR, an outcome that is supported by field studies (Pyle *et al.* 1997; Tettamanti, Witvliet & Bize 2012). In addition to lifespan, other life-history, ecological or social traits may influence the deviation from the age of sexual maturity in the species-specific Optimal AFR. Species could benefit from delayed AFR when there is a high level of parental care (e.g. altricial species), or when requiring time to learn specialized skills to survive or reproduce successfully. Conversely, a prolonged association of juveniles with their parents (i.e. family-living; Drobniak *et al.* 2015) may facilitate skill learning and lead to an earlier species-specific Optimal AFR ('skill hypothesis': Skutch 1961; Langen 1996). An earlier Optimal AFR may also be found in cooperatively-breeding species, since helpers may buffer the reproductive costs of early AFR ('load-lightening hypothesis': Khan & Walters 2002; Santos & Macedo 2011).

Here, we use data from 34 bird species to investigate the extent of variation in reproductive strategies and to assess the potential benefits some species may gain from delaying AFR beyond sexual maturity. We examine interspecific variation in the fitness consequences of AFR using within-species relationships between AFR and a fitness proxy averaged over all individuals within a specific AFR-class. For each of the 34 species, we identified the species- and

sex-specific Optimal AFR and several derived metrics, summarized in Table 1-1, to assess changes in LRS or survival as a function of AFR. Information on species-specific Optimal AFR was previously unavailable for typical meta-analysis approaches due to the substantial challenge of obtaining fitness estimates of populations from several species. Its investigation allows us to make inferences about the selection pressures on AFR that could not be achieved via a simple analysis of interspecific variation in AFR. As a fitness proxy, we used the most commonly provided measure of an individual's productivity, the lifetime number of fledglings or recruits produced (LRS) (Clutton-Brock 1988; Newton 1989 and other references in Table 1-S1). Although it depends on population dynamics, while rate-sensitive fitness estimates (e.g. lambda λ_{ind}) theoretically are more accurate proxies than LRS (Cole 1954; Lewontin 1965; Caswell & Hastings 1980), a number of studies have shown that LRS is a reliable estimate of fitness (Brommer, Merilä & Kokko 2002; Link, Cooch & Cam 2002; Dugdale *et al.* 2010).

Specifically, we addressed the following three questions: (i) How does AFR vary within and among species? (ii) Is variation in AFR associated with differences in LRS, and is the typical AFR of a species the one associated with the highest LRS? (iii) Which life-history (chick developmental mode, LRS and survival change with AFR, lifespan), social (family-living, helper presence) and ecological (latitude, nest predation) factors are associated with among-species variation in deviation of the Optimal AFR from age at maturity? We used a generalized linear mixed model approach in a model selection framework for the analyses, with further control for similarity in phenotype among taxa due to a shared phylogenetic history.

1.2 Materials and Methods

1.2.1 DATA COLLECTION

We used data from published (N = 15) and unpublished (N = 21) studies on the age at first reproduction (AFR) and lifetime reproductive success (LRS) for 34 avian species (Table 1-S1). To

find published data, we searched online databases (ISI Web of Science, Scopus) using the terms "age at first reproduction", "age at first breeding", or "age at maturity" in combination with "lifetime reproductive success", "lifetime reproductive output", or "fitness" and "avian" or "bird". We included data from long-term studies (years of monitoring exceeding the mean lifespan) in which individuals were followed for a sufficient period to accurately measure LRS (mean duration of study: 20.75 years; range: 8 to 48 years) and where LRS (including its mean, standard deviation and sample size) was reported separately for each category of AFR. We used GetData Graph Digitizer 2.25 (http://www.getdata-graph-digitizer.com/) to extract values from published data that were only presented in figures. Unpublished data were requested from researchers who coordinated long-term monitoring studies.

We collected species-specific data on key life-history, ecological and social lifestyle factors that might influence the effect of AFR on LRS (italicized words represents variable names used in the models), including *chick development mode* (altricial or precocial), *mean lifespan*, *mean body mass*, *latitude*, *nest predation risk*, *family-living* and *helper presence*. We also collected data on the age of maturity for the estimation of an index used as variables in the model (see INDICES AND ESTIMATES). Age of maturity corresponded to the age at which an individual is physiologically able to reproduce, or the minimum age recorded for breeders. Among ecological factors that can contribute to nest predation risk, nest location is well known and important (Martin & Li 1992; Martin 1993). Based on this information, we ordinally ranked the nest predation risk as high risk – ground nesters, medium risk – nests in shrubs, low risk – nests in trees, or very low risk – cavity breeders or species that build their nest floating on water and thus difficult for nest predators to access. We considered species to be family-living when offspring remain with the parents beyond independence and non-family living when juveniles disperse soon after becoming independent (Drobniak *et al.* 2015). Species were categorized with helper when offspring regularly engage in cooperative breeding and without helper when offspring do not engage in cooperative breeding. Variables not provided for the populations studied were obtained from the Animal Ageing and

Longevity database (http://genomics.senescence.info/species/) or the Handbooks of the Birds of the World (del Hoyo *et al.* 1992-2006).

1.2.2 DATA COMPOSITION

The 34 species included in our study (Figure 1-S1) comprise 10 taxonomic orders and 22 families, with mean lifespan ranging from 1.4 to 18.5 years and mean LRS ranging from 0.67 to 21.16 fledglings produced over the lifetime, or from 0.54 to 2.53 recruits. For blue tits (*Cyanistes caeruleus*) and western gulls (*Larus occidentalis*), we included data from two different populations that were analyzed separately. While age at first reproduction might be influenced by individual quality (Forslund & Pärt 1995; Kim *et al.* 2011), only few studies provide such information, limiting our ability to include this factor in our analyses. Data collected consisted of average values per species (i.e. body mass) or per AFR age-class category combining data from all cohorts and years. Therefore, annual or cohort variation could not be addressed here but we hope to do so in future work. Note that not controlling for intraspecific individual quality and combining data across cohorts and years is conservative as it reduces the chance of observing biological patterns. Values of mean LRS (N = 34 species) and lifespan (N = 21 species), as well as their standard deviation and sample size (number of individuals), were determined for each AFR age-class category (e.g. from all individuals starting to reproduce at AFR = 1-year old, at AFR = 2, at AFR = 3, and so on), and for each sex if possible. While it would have been more appropriate to use the geometric rather than the arithmetic mean, as it takes into account variability in fitness (see Liou *et al.* 1993), such data were unavailable. Age at first reproduction was defined as the age at which an individual first reproduced during its life. In most species, this value corresponds to the age when a female laid at least one egg, although in some species the value reflects when a female laid a full clutch. For males, AFR corresponds to the age where its mate laid eggs, and, accordingly, reproductively competent males that failed to acquire a mate were not considered as reproductive at that time. The LRS data were based on the number of fledglings or recruits produced over the lifetime of an

individual (Table 1-S1). All LRS values were centered and scaled within species and sexes to convert the original units to those of standard deviations and make them comparable (Schielzeth 2010). For species with only one AFR age-class category, only a single data point was available. Thus we could not estimate the standard deviation necessary for scaling. Instead, we used the standard deviation of the same sex of a species with a similar value of unscaled LRS to calculate the scaled LRS. Accurate estimation of AFR and fitness proxies is challenging as it requires known-aged individuals and intensive individual-based monitoring of reproductive output throughout the lifespan of a representative sample of individuals, as well as data on the survival and reproduction of descendants. Age at first reproduction and fitness proxies may be biased due to extra-pair paternity, or because not all reproductive events of individuals are followed due to emigration from or immigration into the study population. Consequently, AFR might be overestimated and LRS underestimated for males and overestimated for females. Such biases affect the interpretation of the relationship between AFR and fitness components, and add noise to the data. However, because a relation between AFR and extra-pair paternity and or migration has never been documented, we do not know how and to what extent such a bias would affect our interpretation.

1.2.3 INDICES AND ESTIMATES

Interspecific variation in deviations of the Optimal AFR from the age at sexual maturity might be explained by the association of an early or a late AFR with an increase or a decrease in subsequent survival or reproductive output. However, given the heterogeneity of the data distribution between species and sexes, conventional methods are unable to estimate changes in reproductive output or survival with a changing AFR. Thus, we calculated five derived metrics from the raw data per AFR age-class category to investigate this hypothesis (i.e. average values over all individuals from a specific AFR age-class, combining cohorts and years, for each species and where possible split by sex). These included the Delay Index, which assessed the deviations of the Optimal AFR

from the age at sexual maturity, and four indices which assess the relationship between AFR and LRS or survival: the Before Variation Index and the After Variation Index, the Choice Index, and the Lifespan Effect Index (see Table 1-1).

We visually determined the species-specific AFR that maximized LRS ("Optimal AFR"-Table 1-1). The use of a single statistical optimization method was not feasible due to the large diversity of patterns in the relationship between AFR and LRS.

Based on the Optimal AFR, the age at sexual maturity and the latest AFR observed within focal species and sex, we assessed the "Delay Index" representing the timing of the Optimal AFR in relation to the reproductive lifespan (illustrated in Table 1-1):

$$\text{Delay Index} = \frac{\text{Optimal AFR} - \text{maturity age}}{\text{latest AFR} - \text{maturity age}}$$

A Delay Index equal to zero always resulted from the Optimal AFR being the age of maturity.

For 35 out of 62 cases several AFR categories had mean LRS values near that of the Optimal AFR. Hence, we determined the range of the species-specific optimum ages for the onset of reproduction, referred as the "Optimal AFR Range". The Optimal AFR Range included the AFR categories adjacent to the Optimal AFR, with mean LRS values included in the calculation of the standard error bar for the mean LRS of the Optimal AFR (Table 1-1). The AFR categories forming the Optimal AFR Range are therefore assumed to be similarly beneficial in terms of LRS than the Optimal AFR.

Based on the Optimal AFR Range, we estimated the Before Variation Index and the After Variation Index. These indices correspond to the slope of the relationship between LRS and AFR from the earliest and the latest AFR to the center of the Optimal AFR Range. The slopes were estimated in the whole data set with all AFR age-class categories, and in a data set only including categories with more than 5% or 10% of the individuals (Table 1-1). Before and After Variation Indices represent the average of the three estimated slopes. We assumed that a delayed AFR

should be favored if an early AFR is associated with a lower LRS, while an earlier AFR should be favored if a late AFR is associated with a lower LRS. Therefore, we expected the Delay Index to be positively correlated with the Before Variation Index but negatively with the After Variation Index.

Based on the Optimal AFR Range and the actual value observed for the AFR, we calculated the Choice Index (Table 1-1), which represented the probability that individuals adopt AFR(s) with highest fitness return:

$$\text{Choice Index} = \frac{\text{Optimal AFR Range}}{\text{number of AFR categories}}$$

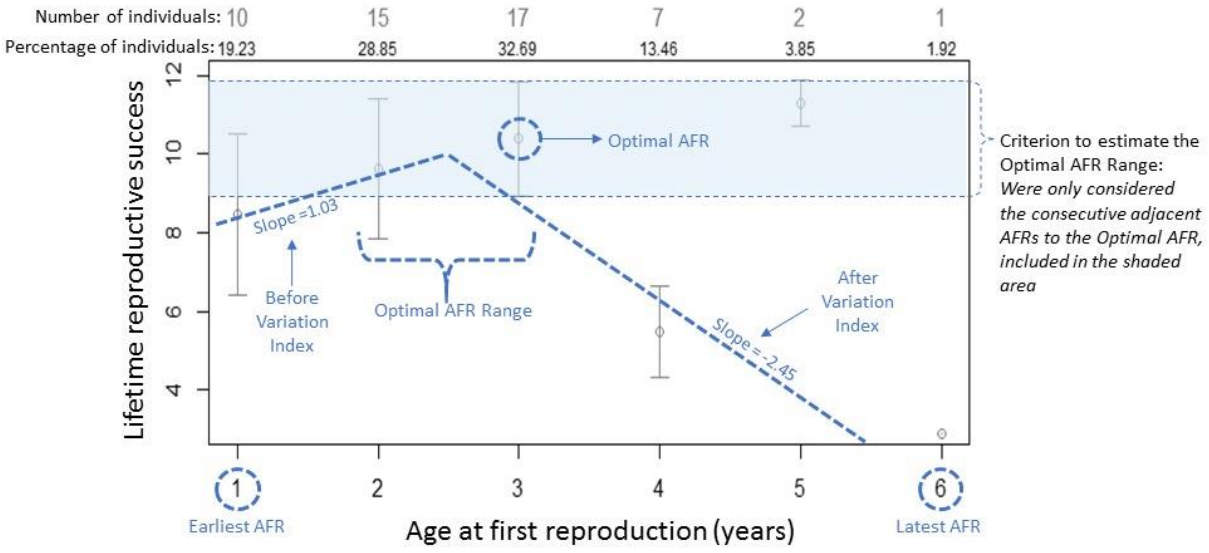
In cases with only one AFR category (N = 6 out of 62 cases), the Choice Index was assigned a zero, as in such cases there is no variation in AFR. We assumed that species with a large Optimal AFR Range relative to the number of AFR categories (i.e. with a large Choice Index) would have a lower probability of suffering a LRS cost when initiating reproduction earlier or later than the Optimal AFR. Consequently, such species may have a higher likelihood of benefiting from delayed reproduction than species with only a low number of beneficial AFR. Therefore, we expected the Delay Index to be positively correlated with the Choice Index.

The association between AFR and subsequent survival was calculated via the Lifespan Effect Index, i.e. the correlation coefficient of the reproductive lifespan plotted against AFR per age-class category. We were able to estimate the Lifespan Effect Index for 21 out of 34 species only, due to missing data for mean lifespan for the different AFR age-class categories for 13 species. As causes and consequences cannot be disentangled from a correlation, negative values could indicate a reproductive cost in terms of survival for individuals with a late AFR or an early AFR favored by high intrinsic mortality. By contrast, positive values could indicate a survival cost of early AFR or a late AFR favored by low intrinsic mortality (Table 1-1, Figure 1-S2). We assumed a survival cost of early AFR to be associated with a late Optimal AFR. Therefore, we expected the Delay Index to be positively correlated with the Lifespan Effect Index.

We verified the robustness of our results based on the indices involving the Optimal AFR Range by considering a second method to estimate it. In this second method, the Optimal AFR Range included AFR(s) adjacent to the Optimal AFR with their 90% CIs overlapping those of the Optimal AFR. The first method (method used in the manuscript abovementioned) represents the logic of a null-hypothesis-like test, which assumes an error distribution around the hypothesis (the Optimal AFR's LRS mean), and if our statistics (the other AFRs' LRS mean) do or do not fall within this range. We also considered this first method to be more straightforward while the use of the second method is more conservative. This is because the use of 90% CI indicates that the LRS population's mean of the focal AFR will fail in 90% of the time, while for the use of the standard error it would do so in around 68% of the time. However, we preferred to present the results from the first method in the manuscript for two reasons. First, most of our data comes from studies with intensive monitoring of a population (Table 1-1, some of which pretty much sample all individuals in the population) and thus, the LRS means approach the population mean with little error. Second, for some AFRs the LRS estimates were based on a single individual (thus without CI). Note that one could prefer to consider one or the other method depending on their data characteristics and questions.

Table 1-1. Definitions and descriptions of the parameters and indices estimated for each sex (when possible) and each species followed by a graph illustrating the description based on the case of the Eurasian sparrowhawk (*Accipiter nisus*). See also Indices and estimates section in Materials and Methods.

Species parameter	Definition	Biological description	Technical description
Optimal AFR	AFR that results in the highest LRS	Reflects the species-average optimum strategy of onset of reproduction	AFR that maximizes mean LRS excluding AFR categories with <10% individuals. Extracted visually
Optimal AFR Range	Range of optimal AFR(s)	Reflects the range of the species-average optimum strategy of onset of reproduction	Number of AFR(s) adjacent to the Optimal AFR with mean LRS values overlapped by the standard error bars of the Optimal AFR. Extracted visually. Range from 1 to 15
Before Variation Index	LRS cost of initiating reproduction before the Optimal AFR Range	Reflects the LRS cost of adopting a reproductive strategy which is earlier than the range of species-average optimum strategy of onset of reproduction	Slope before the Optimal AFR Range (center of the range) between mean LRS and AFR; Average of slopes obtained when all individuals were included, when excluding AFR categories with <5% and <10 % individuals (mean standard error slope = 0.21). A large positive value indicates a strong negative fitness impact of reproducing before the Optimal AFR Range
After Variation Index	LRS cost of initiating reproduction after the Optimal AFR Range	Reflects the LRS cost of adopting a reproductive strategy which is later than the range of species-average optimum strategy of onset of reproduction	Slope after the Optimal AFR Range (center of the range) between mean LRS and AFR; Average of slopes obtained when all individuals were included, when excluding AFR categories with <5% and <10 % individuals (mean standard error slope = 0.18). A large negative value indicates a strong negative fitness impact of reproducing after the Optimal AFR Range
Delay Index	Relative position of the Optimal AFR during the reproductive lifespan	Reflects when – during the average- reproductive lifespan of a species – individuals from a species benefit the most from initiating their reproduction	Varies between 0 and 1. Delay Index 0: the optimal strategy is to start reproduction at physiological maturity; Delay Index 1: the optimal strategy is to delay the onset of reproduction to maximum AFR
Choice Index	Range of optimal AFR(s) relative to the number of AFR observed	Reflects the species-average span of "beneficial choice" in AFR, (i.e. AFRs leading to higher LRS)	Varies between 0 and 1. Choice Index of 0: species has only one optimal AFR; Choice Index of 1: all AFR are optimal
Lifespan Effect Index	Effect of AFR on the mean reproductive lifespan (for each AFR category: see Figure 1-S2)	Reflects the species-specific average effect of the onset of reproduction on survival	Correlation coefficient between mean reproductive lifespan and AFR (Fisher's z transformed) (Koricheva, Gurevitch & Mengersen 2013). Positive values suggest a cost of early onset of reproduction, while negative values suggest a cost of late onset



1.2.4 STATISTICAL ANALYSIS

1.2.4.1 General procedure

All statistical analyses were carried out in R version 3.0.2 ((R Core Team 2013), http://www.R-project.org/) using linear mixed-effects models (lmer function, lme4 package: Bates *et al.* 2014) that allow for the non-independence of data from a single species by including species as a random factor in the model. To account for differences in sample size (N, Table 1-S1) and decrease noise by giving greater emphasis to the more reliable species-specific estimates, all models were weighted (Garamszegi & Møller 2011) by incorporating N-1 in the "weights" argument of the lmer function (Hansen & Bartoszek 2012). Note that removing the weighting did not change the results (Table 1-S2 to 1-S7). To compare coefficients, all continuous predictors were centered (around the mean) and scaled (by the standard deviation) before incorporation in the models (Schielzeth 2010), but we present raw data in the figures. Model assumptions of normality and homogeneity of residuals were checked by visually inspecting histograms and qq-plots of the residuals as well as by plotting residuals against fitted values. For each analysis, we used a model selection process to identify the predictors that best explained variation in the response variable. Model selection was based on minimization of the corrected Akaike's information criterion (AICc) (Burnham & Anderson 2011). Support for an effect of an explanatory variable on the response variable was based on comparison of AICc values between the full model with the effect of interest included vs. excluded, and when ΔAICc ($AICc_{included} - AICc_{excluded}$) was less than or equal to minus five (Burnham & Anderson 2011). The 95% confidence interval (CI) of the predictor estimates was obtained using the confint function (stats package: R Core Team 2013).

The influence of phylogenetic similarity among species was tested in the "best model" obtained during the lmer model selection process (model including only explanatory variables with ΔAICc ≤ -5). This was done by running a phylogenetically controlled mixed-effects model in

ASReml-R (VSN International, Hempstead, U.K.; www.vsn-intl.com) with the same set of predictors as the lmer "best model" for each analysis. The phylogeny was included as a random effect in the form of a correlation matrix of distances from the root of the tree to the most recent common ancestor between two species. The phylogenetic effect was tested by performing a REML likelihood ratio test (comparing the REML likelihood of the same ASReml model with and without phylogeny; the log-likelihood ratio test statistic was assessed against a χ^2 distribution with one degree of freedom). The phylogenetic tree used in this comparative study was adapted from a recent species-level molecular phylogenetic assessment (Jetz *et al.* 2012; Ericson backbone phylogeny) (Figure 1-S1).

1.2.4.2 Variation in age at first reproduction

To determine how AFR varied within and among species, we noted how often an AFR was the most frequently observed AFR within a species (mode) (Figure 1-S3a) and considered the frequency of a specific AFR age-class across all species (Figure 1-S3b). Then, mean AFR and its standard deviation were calculated for each of the 34 species. We tested the influence of sex, mean lifespan and social lifestyle (family-living and presence of helpers) on variation in mean AFR across the 24 species for which we had data for both sexes (Table 1-S1). We used a weighted linear mixed-effect model with population mean AFR as the unit of analysis, and included species as a random effect. Since AFR cannot exceed the mean lifespan, AFR and mean lifespan should be correlated positively. Therefore, we tested whether the estimated correlation between AFR and mean lifespan differed significantly from the null expectation. To do so, we performed a conservative permutation analysis (following Charmantier *et al.* 2006; Lane *et al.* 2011). For each mean lifespan, a mean AFR value was randomly selected with replacement from our dataset. During re-sampling we fixed the rule that AFR was smaller than mean lifespan. Data were re-sampled 500 times and analyzed using the same weighted linear mixed-effect model as described

above. We estimated the average estimates and 95% CIs over the 500 model outputs and compared them to those observed.

1.2.4.3 Fitness consequences of age at first reproduction

To determine whether variation in AFR has consequences for LRS, the correlation between AFR and LRS (within-species) as well as its average influence (among-species effect) was investigated using within-subject centering (van de Pol & Wright 2009). The within-species effect was calculated for each sex and species by subtracting the species- and sex-specific mean AFR from each AFR age-class category observed within sex and species (within-species AFR effect; van de Pol & Wright 2009). The among-species effect was determined as the mean AFR within sex and species (between-species AFR effect; van de Pol & Wright 2009). To test for non-linear effects of AFR on LRS within species, a quadratic term of the within-species AFR effect was included in the model. The AFR values were centered to reduce collinearity between the within-species AFR effect and the within-species AFR^2 effect. Centering enabled independent interpretation of the linear and the curvature effect (Schielzeth 2010). Due to apparent interspecific variation in the relationship between AFR and LRS, the ideal analytical framework would have been a random intercept and slope model that estimated separate intercepts and slopes for each species. However, our sample size did not provide sufficient power to support such a model (Martin *et al.* 2011; van de Pol 2012). Therefore, we ran a standard weighted linear mixed-effect model using the average LRS within AFR age-class categories, with sex and population as units of analysis. Species was included as a random effect in this analysis, along with the natural log of mean body mass as a covariate. We included lifespan in this model as a covariate, since reproductive performance corrected for survival estimates approximates real fitness better (Roff 1992). While the output of the analysis with and without lifespan were similar, lifespan is strongly correlated with the between-species AFR effect. Therefore, we present the analysis without lifespan to avoid issues caused by collinearity (Dormann *et al.* 2013).

To assess whether the most frequently observed AFR within each species was an optimal strategy, the AFR mode within each species was correlated with the AFR that maximized LRS (i.e., Optimal AFR, Table 1-1). Then, the species-specific Optimal AFR was compared to the age at sexual maturity to identify species with optimal delayed reproduction (i.e., species with Optimal AFR > Age at maturity). Finally, the Optimal AFR was correlated with lifespan to identify if a benefit from delaying the onset of reproduction beyond sexual maturity coincided with long lifespan.

1.2.4.4 Among-species variation in the relative timing of optimal age at first reproduction

We used a model selection and model averaging approach (Grueber *et al.* 2011) to determine the factors that explain interspecific variation in deviations of the Optimal AFR from the age of sexual maturity (i.e., Delay Index, Table 1-1). All life-history, social and ecological factors listed above were included (see DATA COLLECTION), as well as indices reflecting the relationship between LRS and AFR: the Choice Index, and the Before and After Variation Indices (see above, Table 1-1). In a second analysis, the Lifespan Effect Index was included for the 21 species for which we had detailed data on lifespan mean for each AFR age-class category (Table 1-1, Figure 1-S2). Due to reduced statistical power of the latter (as on restricted dataset, see above), in the results section we present only the estimates and 95% CI of the analysis excluding the Lifespan Effect Index. Each of the before mentioned variables, and the biologically relevant interactions (Before Variation Index x After Variation Index, Choice Index x Before Variation Index, Choice Index x After Variation Index, Choice Index x Family-living, Choice Index x Helper presence, Mean lifespan x Family-living, Mean lifespan x Helper presence, Nest predation risk x Family-living, Nest predation risk x Helper presence; Table 1-S8 lists predictions associated with these interactions) were tested against the Delay Index in a weighted linear mixed-effect models with Delay Index for each sex and population as a unit of analysis. Species was added as a random effect. Sex and the natural logarithm of body mass were included as default fixed-effects variables to control for allometry and any differences

between sexes. Due to a large number of possible combinations between all predictors, we used the R package MuMIn (Barton 2013) to perform model selection. The candidate model set included models with Δ AICc ≤ 5, Δ AICc being the AICc of the focal model minus the AICc of the best model (see Table 1-S9 for analysis excluding Lifespan Effect Index and Table 1-S10 for analysis including Lifespan Effect Index). To estimate the relative importance of a factor, we summed the Akaike's weights of the models in the set of best models including the focal factor, following the method described by Symonds and Moussalli (2011).

1.3 Results

1.3.1 VARIATION IN AGE AT FIRST REPRODUCTION

Across species (N = 34), age at first reproduction (AFR) ranged from one to 20 years. In 11 species, the modal AFR was one year (Figure 1-S3a). In 70% of species, AFR was age 3 or less and only 20% of species had an AFR that was greater than 6 years of age (Figure 1-S3b). Within species, the number of AFR categories ranged from one to 15 (average = 4.8 years; SD = 3.1; N = 34) and the mean AFR and its standard deviation varied among species (Figure 1-1). Removing sex or social variables (i.e. family-living, helper presence) from the model did not influence mean AFR (Table 1-2). However, mean AFR correlated positively with mean lifespan (parameter estimate for mean lifespan = 0.87, 95% CI (hereafter given in brackets after all estimates): 0.72 to 1.02, Table 1-2), and this correlation exceeded that expected from the mathematical interdependence of AFR and mean lifespan (estimated by the permutation test: mean of 500 simulations: 0.63 (0.87 to 0.79), Δ AICc = -22.24). A positive relationship between AFR and mean lifespan was also apparent when comparing the AFR age-class categories within each species (Figure 1-2). The phylogenetic effect on mean AFR was significant (likelihood ratio test: LRT = 6.99, df = 1, $p < 0.01$).

Table 1-2. Effect of sex, mean lifespan of species, family-living and presence of helpers on mean AFR within a species (N = 26 populations, 24 species for which data were available for both sexes). Estimates and 95% confidence intervals (CI) are presented. **Δ AIC_c corresponds to the change in AIC_c when the specific parameter was included vs. excluded from the full model.**

		Standard deviation	Estimate	95% CI	Δ AIC_c
Fixed effects:					
intercept			0.10	(-0.14, 0.34)	-
sex	Female		0.00	na	-2.51
	Male		0.03	(0.01, 0.05)	
mean lifespan $_{species}$*			0.87	(0.72, 1.02)	-61.65†
family-living	NO		0.00	na	2.58
	YES		-0.12	(-0.89, 0.64)	
helper presence	NO		0.00	na	2.08
	YES		-0.33	(-1.16, 0.50)	
Random effects:					
species		0.52		(0.40, 0.70)	
residuals		0.93		(0.72, 1.26)	

* factor centered and scaled; na – not applicable; † support for inclusion of the factor

1.3.2 FITNESS CONSEQUENCES OF AGE AT FIRST REPRODUCTION

Our within-subject centering approach revealed no among-species effect of AFR on LRS, but a within-species effect of both AFR and AFR^2 (Figure 1-3). Within species, there was strong directional selection for an early AFR (within-species AFR effect estimate = -0.54 (-0.70 to -0.39), Table 1-S11), as well as stabilizing selection (within-species AFR^2 effect estimate = -0.26 (-0.43 to -0.10), Table 1-S11) (Figure 1-3). The phylogenetic effect on mean LRS for the corresponding AFR was not significant (likelihood ratio test: $p = 1$). Twenty-six out of 34 species (76%) had an Optimal AFR delayed beyond the age at maturity, and this delay correlated positively with a longer mean lifespan (slope = 0.28, $r_{Spearman} = 0.61$, $p < 0.005$; Figure 1-4). Both the most-observed AFR and mean AFR correlated with the AFR with the highest LRS (Optimal AFR vs. modal AFR: slope = 0.98, $r_{Spearman} = 0.80$, $p < 0.0001$; Optimal AFR vs. mean AFR: slope = 0.95, $r_{Spearman} = 0.84$, $p < 0.0001$). The latter was true even when only looking at species with a large number of observed AFR age-class categories (Table 1-S12).

Table 1-3. Relative importance of predictors included in the full model for the analysis of Delay Index variation excluding Lifespan Effect Index (N = 36 populations, 34 species) and model averaging estimates (based on 53 models with Δ AICc (AICc focal model – AICc best model) ≤ 5, see Table 1-S9).

Predictors	**Predictor weight***	**Relative importance of predictors †**	**Model averaging estimates‡,§**	**95% CI**
intercept			0.14	(-0.71, 1.00)
ln(body mass)	0.49	1.00	0.35	(0.01, 0.69)
sex	0.49	1.00	Both: 0.00 Female: -0.06 Male: -0.24	na (-0.94, 0.82) (-1.12, 0.65)
Choice Index ¶	0.49	1.00	0.44	(0.15, 0.72)
Before Variation Index ¶	0.48	0.98	0.30	(0.07, 0.54)
family-living	0.40	0.82	NO: 0.00 YES: 0.01	na (-1.45, 1.48)
helper presence	0.40	0.82	NO: 0.00 YES: 0.49	na (-2.12, 3.31)
nest predation risk	0.28	0.56	0.03	(-0.34, 0.43)
Choice Index: helper presence	0.25	0.51	NO: 0.00 YES: -0.67	na (-2.45, -0.18)
mean lifespan	0.25	0.50	0.09	(-0.26, 0.60)
Choice Index: family-living	0.23	0.46	NO: 0.00 YES: 0.57	na (-0.50, 3.00)
mean lifespan: helper presence	0.22	0.44	NO: 0.00 YES: 2.48	na (2.66, 8.49)
mean lifespan: family-living	0.21	0.43	NO: 0.00 YES: -1.91	na (-6.12, -2.72)
nest predation risk: family-living	0.21	0.43	NO: 0.00 YES: 0.91	na (1.23, 2.97)
Before Variation Index: Choice Index	0.17	0.35	0.13	(-0.08, 0.82)
After Variation Index ¶	0.14	0.28	-0.04	(-0.37, 0.05)
nest predation risk: helper presence	0.10	0.21	NO: 0.00 YES: -0.41	na (-3.82, -0.13)
chick development mode	0.05	0.11	Altricial: 0.00 Precocial: -0.02	na (-1.20, 0.74)
latitude	0.03	0.07	-0.01	(-0.41, 0.23)
Before Variation Index: After Variation Index	0.00	0.01	0.00	(-0.08, 0.19)

*: sum of model weights from Table 1-S9 including the focal predictor. na – not applicable;

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.05) (Symonds & Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS and AFR, see Table 1-1 and the Indices and estimates section of Materials and methods.

1.3.3 AMONG-SPECIES VARIATION IN THE RELATIVE TIMING OF OPTIMAL AGE AT FIRST REPRODUCTION

While the Delay Index was associated with indices that reflect a change in LRS and survival as a function of AFR (i.e. Choice, Before Variation and Lifespan Effect Indices; Table 1-1, all predictor weights ≥ 0.45), it was only marginally related to social (predictor weights < 0.45) or ecological factors (predictor weights ≤ 0.30; Tables 1-3 and 1-4). A delayed optimal onset of reproduction (i.e. large Delay Index) was found in species with a large range of optimal AFR relative to reproductive lifespan (Choice Index: estimate = 0.44 (0.15 to 0.72), Table 1-3). Moreover, a large Delay Index was found in species in which early AFR was associated with a decreased LRS (Before Variation Index estimate = 0.30 (0.07 to 0.54), Table 1-3 and Figure 1-3) and a reduced reproductive lifespan (Lifespan Effect Index estimate = 0.54 (0.37 to 0.72), Table 1-4). Finally, larger species showed later optimal onset of reproduction than smaller species (ln (body mass) estimate: 0.35 (0.01 to 0.69), Table 1-3). These results remained quantitatively similar when using indices estimated with the Optimal AFR Range determined under the criterion where AFR categories included in the Optimal AFR Range were AFR(s) adjacent to the Optimal AFR with their 90% CIs overlapping those of the Optimal AFR (Tables 1-S13 to 1-S16).

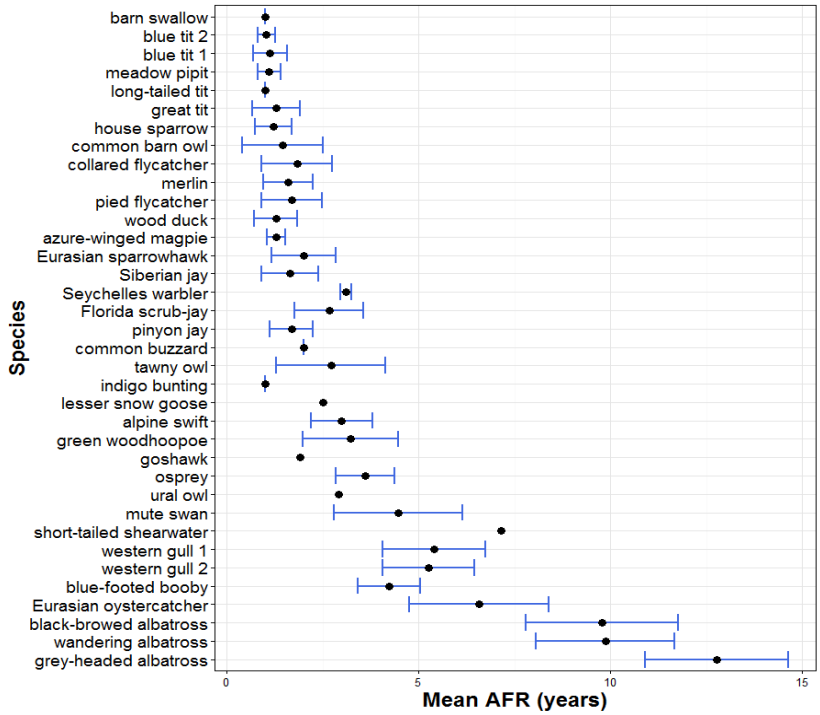


Figure 1-1. Mean AFR (years) and standard deviation for all 36 populations (34 species) (both sexes combined and are ordered by mean LFS). Mean AFR ranged from 1 to 12.8 years (mean ± SD = 3.0 ± 2.6, N = 36), and standard deviation from 0 to 2.31 (mean ± SD = 0.80 ± 0.58, N = 36). A number after the name of a species indicates different populations.

Table 1-4. Relative importance of predictors included in the full model for the analysis of Delay Index variation including Lifespan Effect Index (N = 22 populations, 21 species) and model averaging estimates (based on 28 models with Δ AICc ($AICc_{focal\ model} - AICc_{best\ model}$) ≤ 5, see Table 1-S10).

Predictors	**Predictor weight***	**Relative importance of predictors†**	**Model averaging estimates‡,§**	**95% CI**
intercept			0.42	(-0.34, 1.18)
ln(body mass)	0.57	1.00	0.36	(-0.23, 0.95)
sex	0.57	1.00	Both: 0.00 Female: -0.67 Male: -0.35	na (-1.43, 0.09) (-1.11, 0.42)
Choice Index ¶	0.57	1.00	0.35	(0.17, 0.52)
Lifespan Effect Index ¶	0.57	1.00	0.54	(0.37, 0.72)
After Variation Index ¶	0.38	0.66	-0.20	(-0.56, -0.05)
helper presence	0.26	0.46	NO: 0.00 YES: 0.56	na (0.03, 2.40)
family-living	0.24	0.42	NO: 0.00 YES: -0.32	na (-1.59, 0.08)
mean lifespan	0.23	0.41	0.20	(-0.01, 0.98)
chick development mode	0.10	0.17	Altricial: 0.00 Precocial: -0.11	na (-1.28, 0.04)
nest predation risk	0.10	0.17	0.06	(-0.08, 0.74)
latitude	0.07	0.13	0.02	(-0.32, 0.56)
Choice Index: family-living	0.04	0.07	NO: 0.00 YES: 0.03	na (-0.14, 0.87)
Choice Index: helper presence	0.04	0.07	NO: 0.00 YES: 0.03	na (-0.18, 1.07)
Before Variation Index ¶	0.03	0.06	0.01	(-0.16, 0.35)

*: sum of model weights from Table 1-S10 including the focal predictor. na – not applicable;

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.10) (Symonds & Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting relationship between LRS or survival and AFR, see Table 1-1 and the Indices and estimates section of Materials and methods.

1.4 Discussion

Age at first reproduction (AFR) is a key life-history parameter with consequences for individual reproductive output, and hence its effect on fitness has been studied in a number of intraspecific studies (see references in Table 1-S1). Here we provide a first comparative analysis using a representative amount of averaged within-species information to examine interspecific variation in the relationship between AFR and lifetime reproductive success (LRS). Identifying the species-specific AFR that results in the highest LRS (i.e. Optimal AFR) allowed us to investigate not only within- and among-species variation in the relationship between AFR and LRS, but also differences in the benefits and costs associated with variable timing in the onset of reproduction among species. Our results demonstrated that the most commonly observed AFR within a species corresponds to the species-specific Optimal AFR. Among species, Optimal AFR varied considerably. This study showed that lifespan was a major predictor of the relative timing of the Optimal AFR within the reproductive lifespan and that they correlated positively. Additionally, our analyses revealed that Optimal AFR beyond the age of maturity was associated with a decrease in fitness and survival that arose from starting to reproduce at earlier ages than the Optimal AFR.

Age at first reproduction varied considerably both within and among species (Figure 1-1). Some species displayed no variation in AFR (e.g. long-tailed tit *Aegithalos caudatus*, indigo bunting *Passerina cyanea*, common buzzard *Buteo buteo*), while others exhibited large variation (e.g. mute swan *Cygnus olor*, wandering albatross *Diomedea exulans*, eurasian oystercatcher *Haematopus ostralegus*). Most species that expressed variation in AFR experienced negative consequences for LRS from initiating reproduction either too early or too late in life (e.g. the Optimal AFR was at an intermediate point in the reproductive lifespan: between the age of sexual maturity and the oldest AFR observed within a population), while for others the earliest or latest observed AFR resulted in the highest LRS (Figure 1-3). This suggests simultaneous directional and stabilizing selection. If the pattern observed is a footprint of selection acting at the individual level, this should lead to a

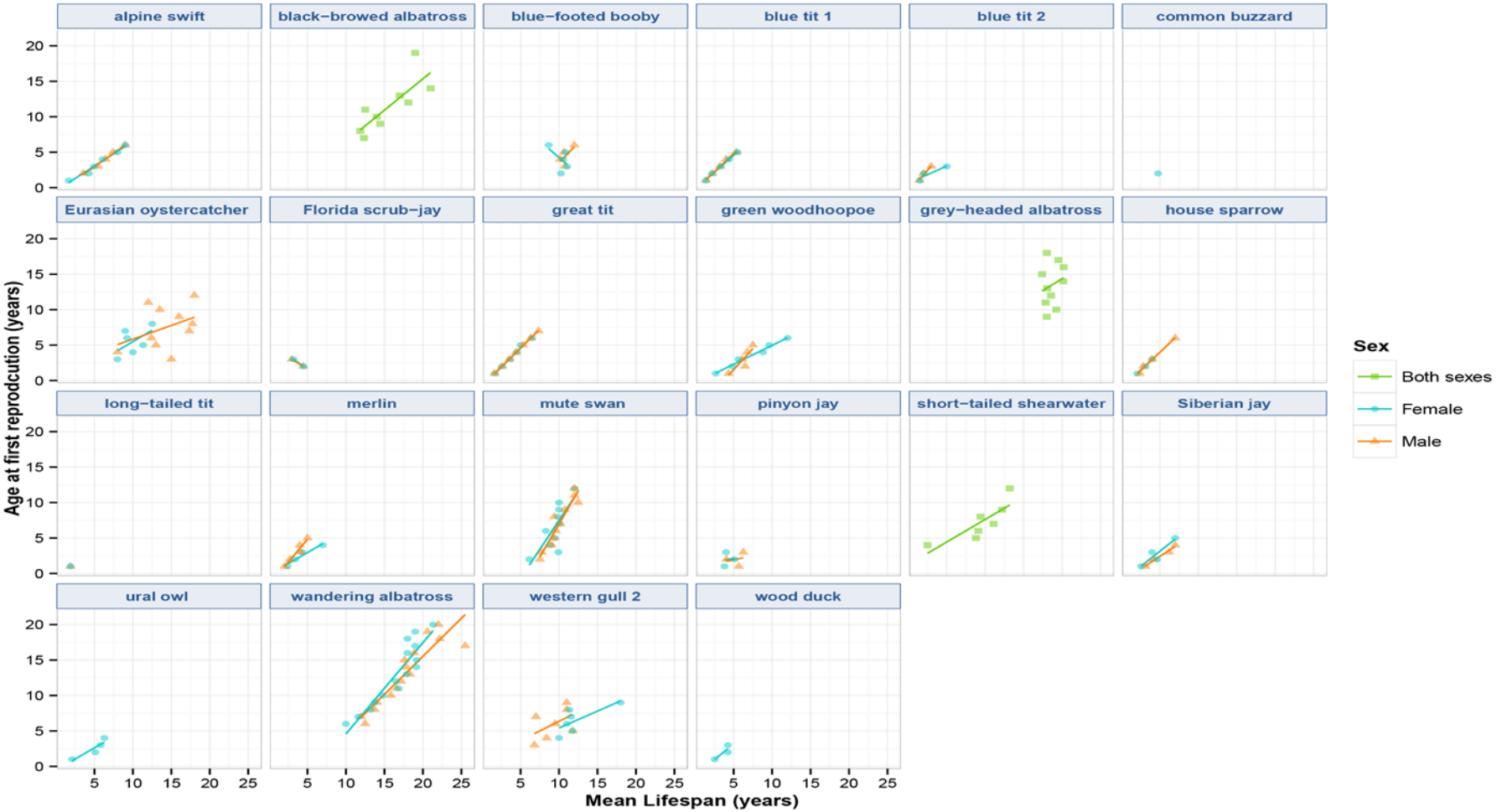


Figure 1-2. Relationship between AFR (years) and the associated mean lifespan within species and sexes (years, N = 22 populations (21 species) for which detailed data on mean lifespan per AFR category were available). Each point is the mean lifespan of individuals within each AFR category. A number after the name of a species indicates different populations. Regression lines are based on the raw data and were drawn for all cases independent of whether the correlation was significant or not.

decrease in average AFR and a reduction in its evolvability. However, a comparative study directly investigating individual variance would be needed to assess this hypothesis.

While there was no overall interspecific relationship between AFR and LRS, a within-species relationship between AFR and LRS (Table 1-S11) indicates that evolutionary processes operate at different scales. On the one hand, large-scale evolution acts on all individuals within a population, which might confound the detection of a relationship between AFR and LRS. On the other hand, local-scale evolution acts on individuals, such as on variation in individual quality (Van Noordwijk & De Jong 1986; Kim *et al.* 2011), food availability (Brommer, Pietiainen & Kolunen 1998), territory quality (Krüger 2005), population density (Krüger 2005) or climatic conditions (Gibbs & Grant 1987; Kim *et al.* 2011), which also might drive the relationship between AFR and LRS. Differences among cohorts in the relationship between AFR and LRS (Brommer, Pietiainen & Kolunen 1998; Kim *et al.* 2011) might additionally explain the absence of a between-species effect of AFR on LRS, but our data did not allow us to take potential differences in individual or cohort quality into account.

Among-species variation in mean AFR correlated positively with lifespan (Table 1-2), supporting the life-history paradigm that the pace of life fundamentally affects reproductive timing (Roff 1992; Stearns 1992; Charlesworth 1994). Furthermore, the species-specific optimal reproductive strategy varied among species, where species with a mean lifespan of up to six years (median mean lifespan: 1.9 years) had an Optimal AFR of one year, providing a quantitative benchmark to differentiate between short- and long-lived bird species. At the other extreme, species with a longer lifespan had a later mean AFR (Table 1-2) and a later Optimal AFR (Figure 1-4).

When relating the position of the Optimal AFR to the age of sexual maturity of a species, our results revealed that the Optimal AFR was beyond the age of maturity in 26 of 34 species.

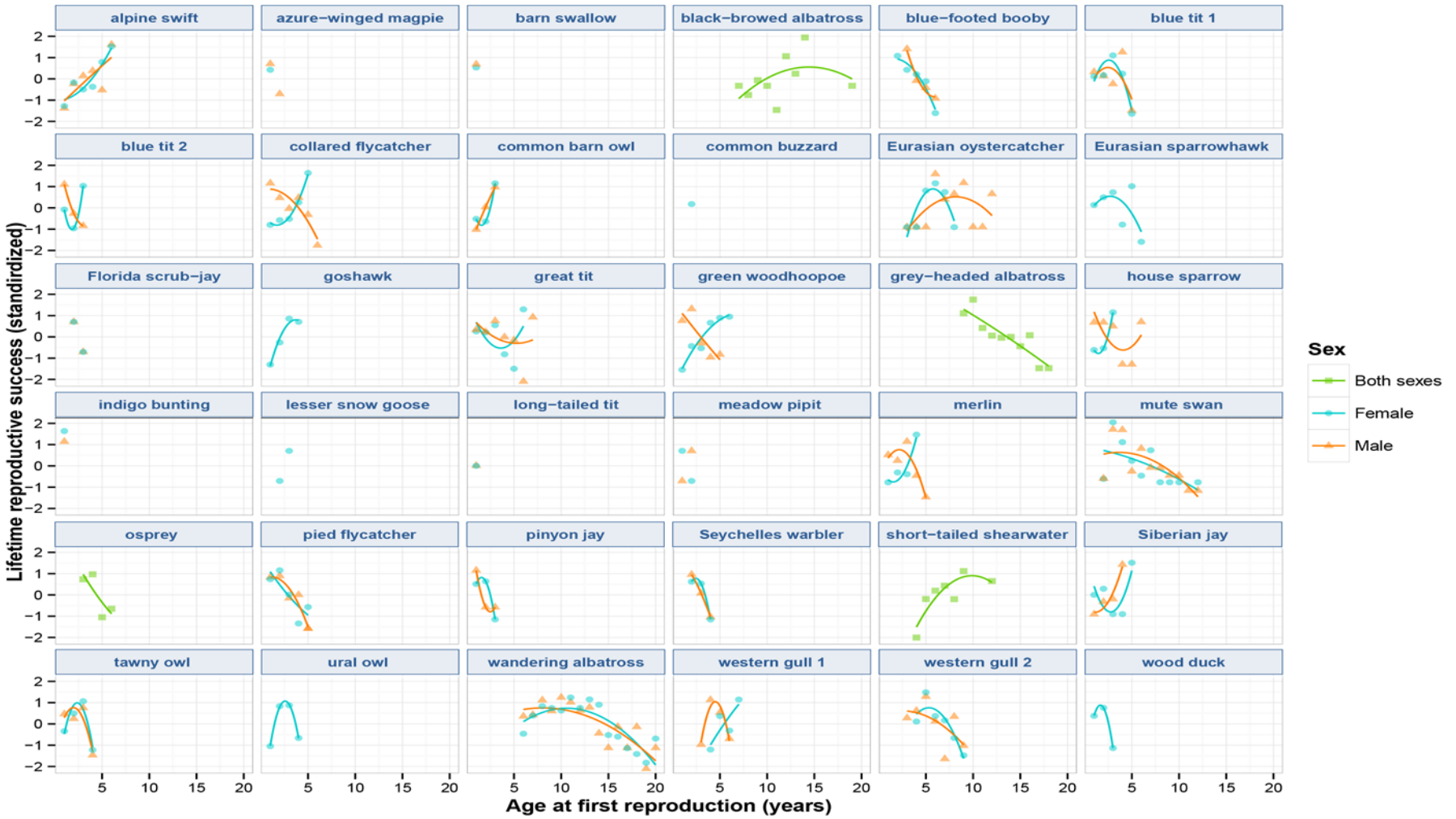


Figure 1-3. Variation in AFR and consequences on fitness - Relationship between standardized LRS and AFR for the 36 populations of the 34 species, separated by sex where possible (a point is the mean LRS (centred and scaled) over all individuals that started to reproduce at a specific AFR). Curves represent quadratic fit of the relationship between standardized LRS and AFR independent of whether the relationship was significant or not.

Thus, individuals in these species appear to benefit from delaying their onset of reproduction (e.g. female tawny owl *Strix aluco* (Millon, Petty & Lambin 2010); female goshawk *Accipiter gentilis* (Krüger 2005); sexes combined short-tailed shearwater *Puffinus tenuirostris* (Wooller *et al.* 1989)). The association of an Optimal AFR beyond the age of sexual maturity with a long mean lifespan suggests that the positive effect of lifespan on mean AFR is not caused by physiological constraints associated with maturity. Indeed, longer-lived species mature later and still adopt an AFR past their age of maturity, and they experienced a larger LRS as a consequence (Figure 1-4). Such a benefit from delayed AFR until after the age of sexual maturity was found not only in long-lived species, but also in six out of 11 short-lived species with a mean lifespan of less than three years (Figure 1-4).

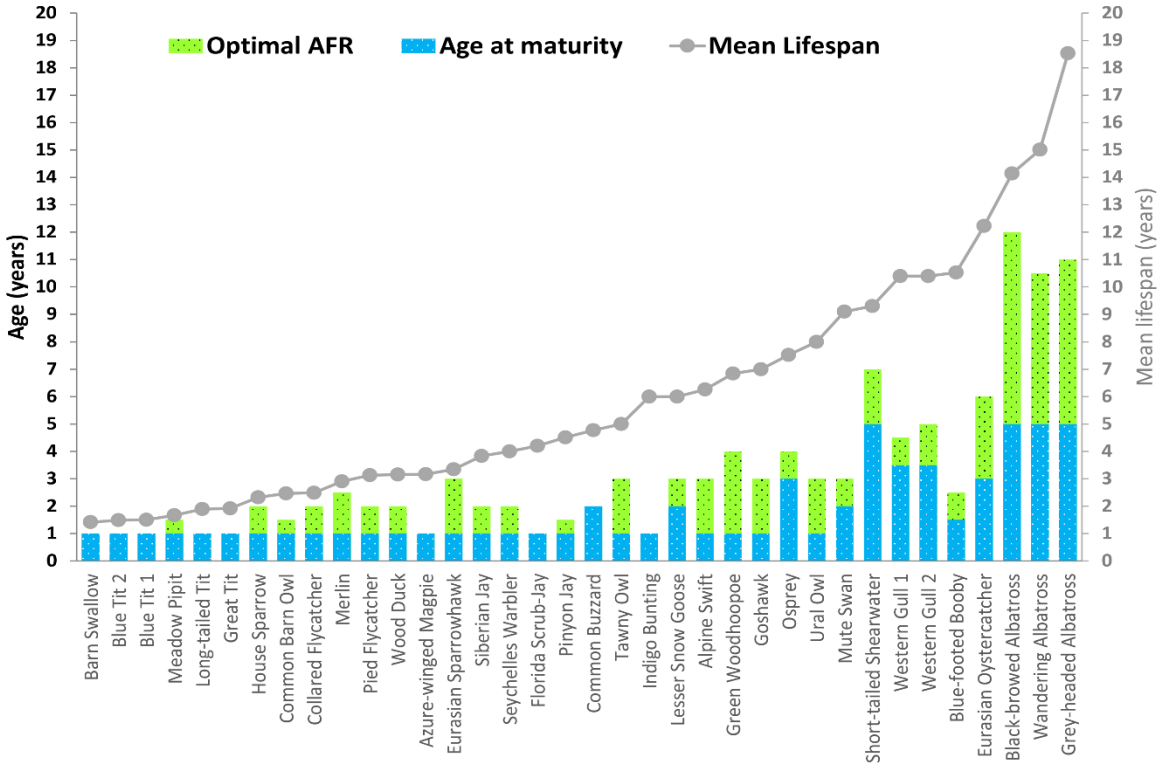


Figure 1-4. Species-specific Optimal AFR presented relative to the species age at maturity (left y-axis) with species ordered by mean lifespan (both sexes combined). Mean lifespan values are represented by the grey line and the right y-axis. A number after the name of a species indicates the different populations included in the study.

When controlling for reproductive lifespan, we found that interspecific variation in deviation of the Optimal AFR from the age at maturity was primarily associated with a change in survival and fitness with AFR (Tables 1-3 and 1-4). Moreover, our results confirmed that an early AFR might be favored by a short reproductive lifespan and vice versa (Roff 1992; Stearns 1992; Charlesworth 1994) (Table 1-4 and Figure 1-2). Species in which an early onset of reproduction was associated with a reduced reproductive lifespan benefited from delaying AFR (Table 1-4 and Figure 1-S2), which supports the restraint hypothesis (Williams 1966; Forslund & Pärt 1995). Moreover, the cost of early reproduction, measured as a decrease in LRS relative to the optimum, correlated positively with the optimal delayed reproductive onset (Table 1-3). An early reproductive onset might be costly because of differences in individual competitive ability, if this early onset leads to unequal probabilities of acquiring a high-quality territory (Ens, Weissing & Drent 1995; Ekman *et al.* 2001; Prevot-Julliard *et al.* 2001; Cooper *et al.* 2009) or to high physiological costs (Hawn, Radford & du Plessis 2007). This pattern suggests that different factors affect the evolution of sexual maturity and the onset of reproduction. Interestingly, in species where there was limited change in LRS relative to AFR, postponing the onset of reproduction beyond sexual maturity was chosen over other earlier AFR leading to similar fitness. Therefore, not reproducing as soon as physiologically capable might provide further benefits. Our results provide empirical support for the hypothesis that costs of reproduction shape the onset of reproduction (Lack 1968; Roff 1992; Stearns 1992).

It has been argued that variation in AFR might be sub-optimal, reflecting constraints on early breeding, such as limited access to high-quality mates or to high-quality breeding sites (Lack 1968; Emlen 1982; Stearns 1989; Koenig *et al.* 1992). However, our results suggest that the onset of reproduction most likely is an optimal strategy, since the most commonly observed AFR coincides with the Optimal AFR. A number of theories developed to explain the evolution of cooperative breeding depicts the decision of offspring to remain with their parents beyond sexual maturity as a “best of a bad job” strategy that reflects dispersal constraints (Emlen 1982; Koenig

et al. 1992; Arnold & Owens 1998; Hatchwell & Komdeur 2000). The lack of a strong correlation between the Delay Index and the different social lifestyles suggests that delayed onset of reproduction might not have evolved due to constraints (Ekman *et al.* 2004; Ekman 2007), but instead constitutes a beneficial life-history decision, which correlates positively with lifespan (Covas & Griesser 2007). Still, the lack of a correlation between social factors and variation in the optimal timing of reproduction could reflect the fact that our data is skewed towards pair-breeding, northern hemisphere species. Including more tropical and southern hemisphere species might alter our results and magnify the role of social factors in our analyses, as the latter two groups are often long-lived (Valcu *et al.* 2014), stay longer with their parents (Russell 2000) and are more likely to breed cooperatively (Jetz & Rubenstein 2011). The current paucity of long-term studies in these regions potentially biases our view of life-history evolution (Martin 2004).

Although we found no significant effect of sex in our study, the relationship between AFR and LRS, and the optimal timing of reproduction, sometimes differed between sexes (Figures 1-3 and 1-S4). Twelve out of 24 species showed sex-specific differences in the Delay Index; females benefited more from earlier onset than males in seven species, whereas the opposite was true in five species (Figure 1-S4). Intraspecific studies have demonstrated sex differences in the relationship between LRS and AFR (e.g. western gull *Larus occidentalis* (Pyle *et al.* 1997); green woodhoopoe *Phoeniculus purpureus* (Hawn, Radford & du Plessis 2007); blue-footed booby *Sula nebouxii* (Kim *et al.* 2011)), highlighting the need to consider sex-specific variation in life-history traits (McDonald 1993; Santos & Nakagawa 2012). The positive correlation between the relative timing of Optimal AFR and body mass concurs with findings in mammals where AFR is correlated strongly with body mass (larger mammals having later AFR; Estern 1979; Wootton 1987). Nevertheless, we additionally demonstrated that, in birds, larger species benefited more from delaying the onset of reproduction beyond sexual maturity than smaller species. Therefore, body mass seems to be an important factor associated with variation in reproductive strategy. Animals with a large body size invest substantial amounts of resources into growth. Although, in birds,

growth after sexual maturity is negligible (Ricklefs 1983), postponing the onset of reproduction might counterbalance the cost endured during the development phase and increase the probability of a high lifetime reproductive output.

In conclusion, AFR varies both within and among species, and this variation is reflected in LRS. The most frequently observed AFR within a species results in the highest LRS. Where an AFR delayed beyond physiological maturity co-occurred with the highest LRS, this delay was mainly associated with a long lifespan and a decrease in LRS and future survival linked to early reproduction. Our study is the first to provide empirical confirmation of several key predictions of life-history theory across species that lifespan and costs of reproduction shape reproductive timing (Lack 1968; Roff 1992; Stearns 1992; Charlesworth 1994). Moreover, the finding that, in long-lived species, postponing the onset of independent reproduction is an optimal strategy has important implications for long-held perspectives on the evolution of sociality. Hitherto, the decision of young birds to remain with their parents and become helpers has been viewed as a sub-optimal response to the lack of breeding opportunities (Emlen 1982; Koenig *et al.* 1992; Arnold & Owens 1998). Our results clearly indicate that this decision can be a strategy to mitigate the costs of early reproduction. Overall, our results are consistent with life-history theory and challenge current theories on the evolution of family formation and cooperative breeding.

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Appendix Chapter 1

Table 1-S1. Information on the source and the type of LRS data for each study.

Species	Scientific name	Location	LRS type	Sample size*	Reference
alpine swift	*Apus melba*	North-Western Switzerland	fledglings	F: 157; M: 121	**Pierre Bize**
azure-winged magpie	*Cyanopica cyanus*	Valdesequera, Spain	fledglings	F: 200; M: 104	**Juliana Valencia & Carlos de la Cruz**
barn swallow	*Hirundo rustica*	Kraghede, Denmark	fledglings	F: 1394; M: 1360	**Anders Pape Møller**
black-browed albatross	*Thalassarche melanophris*	Bird Island, UK	fledglings	B: 76	**Richard Phillips & Andrew G. Wood**
blue Tit 1	*Cyanistes caeruleus*	Oxford, UK	recruits	F: 1177; M: 972	**Sandra Bouwhuis & Ben Sheldon**
blue Tit 2	*Cyanistes caeruleus*	Vienna, Austria	recruits	F: 261; M: 211	**Bart Kempenaers & Emmi Schlicht**
blue-footed booby	*Sula nebouxii*	Isla Isabela, Mexico	fledglings	F: 222; M: 246	Kim et al. (2011)
collared flycatcher	*Ficedula albicollis*	Budapest, Hungary	recruits	F: 453; M: 481	**Márton Herényi & János Török**
common barn owl	*Tyto alba*	Payerne, Switzerland	fledglings	F: 170; M: 174	**Alexandre Roulin**
common buzzard	*Buteo buteo*	Eastern Westphalia, Germany	fledglings	F: 239	**Olivier Krüger**
Eurasian sparrowhawk	*Accipiter nisus*	Annandale, Eskdale, Scotland	fledglings	F: 52	McGraw & Caswell (1996)
Eurasian oystercatcher	*Haematopus ostralegus*	Schiermonnikoog, Netherlands	fledglings	F: 19; M: 33	**Martijn Van de Pol**
Florida scrub-jay	*Aphelocoma coerulescens*	Archbold, USA	fledglings	F: 37; M: 43	Fitzpatrick & Woolfenden (1988)
goshawk	*Accipiter gentilis*	Bissendorf, Spenge, Germany	fledglings	F: 74	Krüger (2005)
great tit	*Parus major*	Oxford, UK	recruits	F: 4935; M: 4370	**Sandra Bouwhuis & Ben Sheldon**
green woodhoopoe	*Phoeniculus purpureus*	Eastern Cape, South Africa	fledglings	F: 59; M: 62	**Andrew Radford**
grey-headed albatross	*Thalassarche chrysostoma*	Bird Island, UK	fledglings	B: 74	**Richard Phillips & Andrew G. Wood**
house sparrow	*Passer domesticus*	Lundy Island, UK	fledglings	F: 287; M: 265	**Terry Burke & colleagues**
indigo bunting	*Passerina cyanea*	Southern Michigan, USA	fledglings	F: 360; M: 357	Payne (1989)
lesser snow goose	*Chen caerulescens*	La Perouse Bay, Canada	1st 4 years of life	F: 2616	Viallefont et al. (1995)
long-tailed tit	*Aegithalos caudatus*	Sheffield, UK	recruits	F: 119; M: 109	**Ben Hatchwell**
meadow pipit	*Anthus pratensis*	North-west Germany	fledglings	F: 33; M: 49	**Hermann Hötker**
merlin	*Falco columbarius*	Saskatoon, Canada	fledglings	F: 26; M: 68	**Richard Espie & Ian G. Warkentin**
mute swan	*Cygnus olor*	Abbotsbury, UK	recruits	F: 252; M: 277	**Anne Charmantier, Ben Sheldon & Chris Perrins**
osprey	*Pandion haliaetus*	Michigan, USA	fledglings	B: 40	Postupalsky (1989)
pied flycatcher	*Ficedula hypoleuca*	Wolfsburg, Germany	fledglings	F: 1411; M: 1135	Sternberg (1989)
pinyon jay	*Gymnorhinus cyanocephalus*	Flagstaff, USA	yearlings	F: 39; M: 41	**John Marzluff**
Seychelles warbler	*Acrocephalus sechellensis*	Cousin Island, Seychelles	fledglings	F: 41; M: 37	Komdeur (1996)
short-tailed shearwater	*Puffinus tenuirostris*	Fisher Island, Australia	fledglings	B: 186	Wooller et al. (1989)
Siberian jay	*Perisoreus infaustus*	Arvidsjaur, Sweden	fledglings	F: 44; M: 56	Ekman & Griesser (2016b)
tawny owl	*Strix aluco*	Kielder Forest, UK	fledglings	F: 83; M: 51	Millon et al. (2010)
ural owl	*Strix uralensis*	Päijät-Häme, Finland	fledglings	F: 57	Brommer et al. (1998)
wandering albatross	*Diomedea exulans*	Bird Island, UK	fledglings	F: 1819; M: 1519	**Richard Phillips & Andrew G. Wood**
western gull 1	*Larus occidentalis*	Farallon Island, USA	fledglings	F: 163; M: 108	Pyle et al. (1997)
western gull 2	*Larus occidentalis*	Farallon Island, USA	fledglings	F: 66; M: 93	**Russell Bradley**
wood duck	*Aix sponsa*	South Carolina, USA	fledglings	F: 90	Oli et al. (2002)

Bold reference indicates unpublished data provided directly by researchers.* number of individuals of F: female, M: male, B: both sexes

Table 1-S2. Model without weighting (see Table 1-2 for output model with weighting) - Effect of sex, mean lifespan of species, family-living and presence of helpers on mean AFR within a species (N = 26 populations, 24 species for which data were available for both sexes). Estimates and 95% confidence intervals (CI) are presented. Δ AICc corresponds to the change in AICc when the specific parameter was included vs. excluded from the full model.

		Standard deviation	Estimate	95% CI	Δ AIC_c
Fixed effects:					
intercept			0.10	(-0.14, 0.34)	-
sex	Female		0.00	na	1.99
	Male		0.02	(-0.03, 0.07)	
mean lifespan $_{species}$*			0.82	(0.67, 0.96)	-58.68†
family-living	NO		0.00	na	2.60
	YES		-0.11	(-0.87, 0.66)	
helper presence	NO		0.00	na	2.07
	YES		-0.34	(-1.18, 0.50)	
Random effects:					
species		0.52		(0.40, 0.70)	
residuals		0.09		(0.07, 0.12)	

* factor centered and scaled; na – not applicable; † support for inclusion of the factor

Table 1-S3. Model without weighting (see Table 1-S11 for output model with weighting). Results from models testing the within- and among-species effect of AFR on LRS (N = 36 populations, 34 species). Estimates and 95% confidence intervals (CI) are presented. Δ AICc corresponds to the change in AICc when the specific parameter was included vs. excluded from the full model.

		Standard deviation	Estimate	95% CI	Δ AIC_c
Fixed effects:					
intercept			0.00	(-0.36, 0.37)	-
ln(body mass)*			-0.01	(-0.17, 0.14)	2.10
sex	Both		0.00	na	3.76
	Female		0.12	(-0.28, 0.54)	
	Male		0.14	(-0.26, 0.54)	
within-species AFR*			-0.38	(-0.56, -0.20)	-14.97†
within-species AFR^2*			-0.30	(-0.51, -0.10)	-6.36†
between-species AFR			0.03	(-0.16, 0.22)	2.03
Random effects:					
species		0.00		(0.00, 0.13)	
residuals		0.86		(0.79, 0.93)	

* factor centered and scaled; na – not applicable; † support for inclusion of the factor

Table 1-S4. Model without weighting (see Table 1-3 for output model with weighting). Relative importance of predictors included in the full model for the analysis of Delay Index variation excluding Lifespan Effect Index (N = 36 populations, 34 species) and model averaging estimates (based on 58 models with Δ AICc ($AICc_{focal\ model} - AICc_{best\ model}$) ≤ 5, see Table 1-S6).

Predictors	**Predictor weight***	**Relative importance of predictors†**	**Model averaging estimates‡,§**	**95% CI**
intercept			0.07	(-0.78, 0.92)
ln(body mass)	0.49	1.00	0.36	(0.08, 0.64)
sex	0.49	1.00	Both: 0.00 Female: -0.01 Male: -0.05	na (-0.92, 0.89) (-0.97, 0.87)
Choice Index ¶	0.49	1.00	0.59	(0.34, 0.85)
Before Variation Index ¶	0.48	0.98	0.30	(0.08, 0.52)
Before Variation Index: Choice Index	0.34	0.70	0.25	(0.01, 0.71)
latitude	0.17	0.35	-0.06	(-0.42, 0.06)
After Variation Index ¶	0.12	0.25	-0.03	(-0.31, 0.09)
mean lifespan	0.10	0.20	0.04	(-0.16, 0.54)
family-living	0.08	0.16	NO: 0.00 YES: -0.03	na (-0.65, 0.31)
nest predation risk	0.07	0.14	0.01	(-0.20, 0.31)
helper presence	0.06	0.12	NO: 0.00 YES: -0.00	na (-0.69, 0.66)
chick development mode	0.05	0.11	Altricial: 0.00 Precocial: 0.00	na (-0.75, 0.76)
Choice Index: family-living	0.01	0.03	NO: 0.00 YES: 0.02	na (-0.42, 1.38)
After Variation Index: Choice Index	0.01	0.02	0.00	(-0.15, 0.34)
Before Variation Index: After Variation Index	0.01	0.02	-0.00	(-0.17, 0.11)
mean lifespan: helper presence	0.00	0.01	0.01	(-0.26, 2.12)
Choice Index: helper presence	0.00	0.01	NO: 0.00 YES: -0.01	na (-1.99, -0.14)

*: sum of model weights from Table 1-S6 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.04) (Symonds & Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS and AFR, see Table 1-1 and the Indices and estimates section of Materials and methods.

Table 1-S5. Model without weighting (see Table 1-4 for output model with weighting). Relative importance of predictors included in the full model for the analysis of Delay Index variation including Lifespan Effect Index (N = 22 populations, 21 species) and model averaging estimates (based on 28 models with Δ AICc ($AICc_{focal\ model} - AICc_{best\ model}$) ≤ 5, see Table 1-S7).

Predictors	**Predictor weight***	**Relative importance of predictors†**	**Model averaging estimates‡,§**	**95% CI**
intercept			0.16	(-0.67, 0.99)
ln(body mass)	0.51	1.00	0.24	(-0.44, 0.92)
sex	0.51	1.00	Both: 0.00 Female: -0.26 Male: -0.03	na (-1.17, 0.65) (-0.92, 0.87)
Lifespan Effect Index ¶	0.51	1.00	0.54	(0.32, 0.77)
Choice Index ¶	0.49	0.96	0.32	(0.07, 0.60)
mean lifespan	0.30	0.59	0.33	(0.02, 0.10)
After Variation Index ¶	0.25	0.48	-0.13	(-0.51, -0.03)
helper presence	0.24	0.47	NO: 0.00 YES: 0.47	na (-0.10, 2.06)
family-living	0.18	0.35	NO: 0.00 YES: -0.26	na (-1.57, 0.08)
latitude	0.08	0.15	-0.04	(-0.60, 0.06)
mean lifespan: helper presence	0.05	0.10	0.15	(0.21, 2.82)
Choice Index: family-living	0.05	0.09	NO: 0.00 YES: 0.04	na (-0.01, 0.95)
Choice Index: helper presence	0.04	0.08	NO: 0.00 YES: 0.04	na (-0.04, 1.04)
Before Variation Index ¶	0.03	0.05	0.01	(-0.16, 0.34)
chick development mode	0.03	0.05	Altricial: 0.00 Precocial: -0.02	na (-1.00, 0.22)
nest predation risk	0.02	0.03	0.00	(-0.32, 0.34)

*: sum of model weights from Table 1-S7 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.08) (Symonds & Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS or survival and AFR, see Table 1-1 and the Indices and estimates section of Materials and methods.

Table 1-S6. Model without weighting (see Table 1-S9 for output model with weighting). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	Sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.20	0.42	+	-	-	-	-	-	-	0.63	0.30	-	-	-	0.34	-	-	-	-	-	-	9	-68.56	158.58	0.00	0.04
-0.06	0.37	+	-0.17	-	-	-	-	-	0.64	0.34	-	-	-	0.35	-	-	-	-	-	-	10	-67.44	159.19	0.61	0.03
0.14	0.40	+	-	-	-	-	-	-	0.50	0.23	-	-	-	-	-	-	-	-	-	-	8	-70.52	159.75	1.17	0.02
0.05	0.28	+	-	-	-	-	0.20	-	0.65	0.31	-	-	-	0.34	-	-	-	-	-	-	10	-67.80	159.91	1.33	0.02
0.25	0.40	+	-	-	-	-	-	-	0.62	0.31	-0.10	-	-	0.35	-	-	-	-	-	-	10	-68.07	160.45	1.87	0.02
-0.12	0.35	+	-0.17	-	-	-	-	-	0.51	0.27	-	-	-	-	-	-	-	-	-	-	9	-69.52	160.49	1.92	0.02
0.19	0.35	+	-	0.12	-	-	-	-	0.64	0.32	-	-	-	0.41	-	-	-	-	-	-	10	-68.10	160.52	1.94	0.02
-0.03	0.34	+	-0.19	-	-	-	-	-	0.63	0.35	-0.11	-	-	0.36	-	-	-	-	-	-	11	-66.71	160.70	2.12	0.01
0.20	0.42	+	-	-	+	-	-	-	0.62	0.29	-	-	-	0.35	-	-	-	-	-	-	10	-68.29	160.90	2.32	0.01
-0.02	0.25	+	-	-	-	-	0.20	-	0.52	0.25	-	-	-	-	-	-	-	-	-	-	9	-69.77	161.00	2.42	0.01
-0.09	0.37	+	-0.19	-	+	-	-	-	0.63	0.33	-	-	-	0.36	-	-	-	-	-	-	11	-66.94	161.15	2.57	0.01
0.08	0.22	+	-	-	-	-	0.24	-	0.64	0.33	-0.12	-	-	0.35	-	-	-	-	-	-	11	-67.00	161.29	2.71	0.01
0.22	0.41	+	-	-	-	-	-	+	0.63	0.30	-	-	-	0.36	-	-	-	-	-	-	10	-68.54	161.39	2.81	0.01
0.20	0.42	+	-	-	-	+	-	-	0.63	0.30	-	-	-	0.34	-	-	-	-	-	-	10	-68.56	161.43	2.85	0.01
-0.10	0.34	+	-0.21	-	-	+	-	-	0.63	0.33	-	-	-	0.35	-	-	-	-	-	-	11	-67.18	161.64	3.07	0.01
-0.03	0.32	+	-0.19	-	-	-	-	+	0.66	0.34	-	-	-	0.41	-	-	-	-	-	-	11	-67.21	161.70	3.12	0.01
-0.04	0.33	+	-0.15	0.08	-	-	-	-	0.64	0.35	-	-	-	0.39	-	-	-	-	-	-	11	-67.25	161.78	3.20	0.01
0.25	0.29	+	-	0.16	-	-	-	-	0.64	0.35	-0.13	-	-	0.44	-	-	-	-	-	-	11	-67.25	161.78	3.20	0.01
0.17	0.38	+	-	-	-	-	-	-	0.50	0.24	-0.08	-	-	-	-	-	-	-	-	-	9	-70.17	161.81	3.23	0.01
-0.08	0.31	+	-0.13	-	-	-	0.10	-	0.64	0.33	-	-	-	0.35	-	-	-	-	-	-	11	-67.29	161.86	3.28	0.01

Table 1-S6 following. Model without weighting (see Table 1-S9 for output model with weighting). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	Sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likihood	AICc	Δ AICc	weight
-0.01	0.48	+	-	-	-	-	-	-	0.49	-	-	-	-	-	-	-	-	-	-	-	7	-72.98	162.03	3.45	0.01
0.09	0.44	+	-	-	-	-	-	+	0.50	0.24	-	-	-	-	-	-	-	-	-	-	9	-70.30	162.05	3.47	0.01
0.18	0.43	+	-	-	+	-	-	-	0.54	0.28	-	-	-	0.34	-	+	-	-	-	-	11	-67.39	162.06	3.48	0.01
0.13	0.40	+	-	-	+	-	-	-	0.50	0.23	-	-	-	-	-	-	-	-	-	-	9	-70.34	162.15	3.57	0.01
-0.10	0.32	+	-0.18	-	-	-	-	-	0.50	0.28	-0.10	-	-	-	-	-	-	-	-	-	10	-68.99	162.29	3.71	0.01
0.13	0.39	+	-	0.02	-	-	-	-	0.50	0.24	-	-	-	-	-	-	-	-	-	-	9	-70.50	162.47	3.89	0.01
0.13	0.40	+	-	-	-	+	-	-	0.50	0.23	-	-	-	-	-	-	-	-	-	-	9	-70.51	162.49	3.91	0.01
0.06	0.29	+	-	-	+	-	0.18	-	0.64	0.30	-	-	-	0.35	-	-	-	-	-	-	11	-67.64	162.56	3.98	0.01
-0.15	0.35	+	-0.18	-	+	-	-	-	0.50	0.26	-	-	-	-	-	-	-	-	-	-	10	-69.16	162.64	4.06	0.01
0.01	0.20	+	-	-	-	-	0.24	-	0.52	0.26	-0.11	-	-	-	-	-	-	-	-	-	10	-69.17	162.66	4.08	0.01
-0.06	0.34	+	-0.21	-	+	-	-	-	0.63	0.35	-0.11	-	-	0.37	-	-	-	-	-	-	12	-66.20	162.77	4.19	0.01
0.08	0.28	+	-	0.05	-	-	0.16	-	0.65	0.32	-	-	-	0.37	-	-	-	-	-	-	11	-67.75	162.77	4.20	0.01
-0.08	0.29	+	-0.24	-	-	+	-	-	0.63	0.35	-0.13	-	-	0.37	-	-	-	-	-	-	12	-66.23	162.82	4.24	0.01
0.26	0.40	+	-	-	-	-	-	-	0.62	0.31	-0.12	-	0.10	0.39	-	-	-	-	-	-	11	-67.77	162.83	4.25	0.01
0.06	0.27	+	-	-	-	+	0.20	-	0.65	0.31	-	-	-	0.34	-	-	-	-	-	-	11	-67.79	162.87	4.29	0.00
0.05	0.28	+	-	-	-	-	0.20	+	0.65	0.31	-	-	-	0.34	-	-	-	-	-	-	11	-67.80	162.87	4.29	0.00
0.01	0.27	+	-0.16	0.12	-	-	-	-	0.64	0.38	-0.14	-	-	0.43	-	-	-	-	-	-	12	-66.25	162.88	4.30	0.00
0.24	0.40	+	-	-	+	-	-	-	0.62	0.30	-0.09	-	-	0.36	-	-	-	-	-	-	11	-67.82	162.91	4.33	0.00
0.16	0.46	+	-	-	+	+	-	-	0.62	0.30	-	-	-	0.35	-	-	-	-	-	-	11	-67.85	162.98	4.40	0.00
-0.15	0.33	+	-0.20	-	-	+	-	-	0.51	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.34	162.99	4.41	0.00

Table 1-S6 following. Model without weighting (see Table 1-S9 for output model with weighting). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	Sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likihood	AICc	Δ AICc	weight
-0.14	0.28	+	-0.13	-	-	-	0.11	-	0.52	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.35	163.01	4.43	0.00
0.19	0.36	+	-	0.11	+	-	-	-	0.64	0.32	-	-	-	0.41	-	-	-	-	-	-	11	-67.87	163.01	4.44	0.00
-0.10	0.29	+	-	-	-	-	0.22	+	0.52	0.26	-	-	-	-	-	-	-	-	-	-	10	-69.39	163.08	4.51	0.00
0.11	0.41	+	-	-	+	-	-	-	0.41	0.21	-	-	-	-	-	+	-	-	-	-	10	-69.39	163.09	4.51	0.00
-0.13	0.37	+	-0.16	-	-	-	-	+	0.51	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.46	163.24	4.66	0.00
-0.05	0.25	+	-0.14	-	-	-	0.14	-	0.64	0.35	-0.12	-	-	0.36	-	-	-	-	-	-	12	-66.44	163.25	4.67	0.00
0.25	0.40	+	-	-	-	-	-	-	0.63	0.33	-0.09	-0.03	-	0.35	-	-	-	-	-	-	11	-67.98	163.25	4.67	0.00
-0.01	0.35	+	-0.19	-	-	-	-	-	0.63	0.35	-0.14	-	0.09	0.39	-	-	-	-	-	-	12	-66.44	163.25	4.67	0.00
-0.12	0.36	+	-0.17	-0.02	-	-	-	-	0.51	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.50	163.32	4.74	0.00
0.25	0.39	+	-	-	-	+	-	-	0.62	0.31	-0.10	-	-	0.36	-	-	-	-	-	-	11	-68.06	163.40	4.82	0.00
0.26	0.39	+	-	-	-	-	-	+	0.63	0.31	-0.09	-	-	0.36	-	-	-	-	-	-	11	-68.06	163.41	4.83	0.00
0.00	0.29	+	-0.21	-	-	-	-	+	0.65	0.36	-0.11	-	-	0.41	-	-	-	-	-	-	12	-66.53	163.43	4.85	0.00
0.18	0.36	+	-	0.13	-	-	-	+	0.64	0.33	-	-	-	0.40	-	-	-	-	-	-	11	-68.09	163.46	4.88	0.00
0.19	0.35	+	-	0.12	-	+	-	-	0.64	0.33	-	-	-	0.41	-	-	-	-	-	-	11	-68.10	163.48	4.90	0.00
-0.03	0.34	+	-0.19	-	-	-	-	-	0.64	0.37	-0.10	-0.04	-	0.36	-	-	-	-	-	-	12	-66.57	163.50	4.92	0.00
0.11	0.28	+	-	-	-	+	0.16	-	0.60	0.29	-	-	-	0.33	-	-	+	-	-	-	12	-66.58	163.52	4.94	0.00
-0.04	0.26	+	-	-0.08	-	-	0.26	-	0.53	0.24	-	-	-	-	-	-	-	-	-	-	10	-69.61	163.53	4.95	0.00
0.02	0.48	+	-	-	+	+	-	-	0.42	0.20	-	-	-	-	+	+	-	-	-	-	12	-66.59	163.54	4.96	0.00

Model set with Δ AICc ≤ 5. N = 36 populations, 34 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models.

Table 1-S7. Model without weighting (see Table 1-S10 for output model with weighting). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	Lifespan Effect Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	logLikelihood	AICc	Δ AICc	weight
0.11	-0.07	+	-	-	-	-	0.66	-	0.36	-	-0.27	0.54	-	-	-	-	-	-	10	-30.40	89.61	0.00	0.08
0.31	0.65	+	-	-	+	+	-	-	0.35	-	-	0.57	-	-	-	-	-	-	10	-31.00	90.79	1.19	0.05
0.31	0.60	+	-	-	+	+	-	-	0.20	-	-	0.52	-	-	+	-	-	-	11	-29.15	91.29	1.69	0.04
0.08	0.17	+	-	-	-	-	0.47	-	0.40	-	-	0.56	-	-	-	-	-	-	9	-33.33	91.59	1.99	0.03
0.36	0.56	+	-	-	+	+	-	-	0.22	-	-	0.57	-	+	-	-	-	-	11	-29.38	91.76	2.15	0.03
-0.08	0.43	+	-0.31	-	-	-	-	-	0.40	-	-	0.54	-	-	-	-	-	-	9	-33.56	92.04	2.44	0.02
0.03	-0.03	+	-	-	-	-	0.70	+	0.36	-	-0.33	0.52	-	-	-	-	-	-	11	-29.56	92.12	2.52	0.02
-0.12	-0.03	+	-0.19	-	-	-	0.54	-	0.37	-	-0.27	0.53	-	-	-	-	-	-	11	-29.58	92.16	2.56	0.02
0.18	-0.06	+	-	-	-	+	0.59	-	0.28	-	-0.28	0.51	-	-	-	+	-	-	12	-27.39	92.36	2.75	0.02
0.09	0.01	+	-	-	-	+	0.62	-	0.39	-	-0.27	0.52	-	-	-	-	-	-	11	-29.71	92.41	2.81	0.02
0.45	0.52	+	-	-	-	-	-	-	0.38	-	-	0.56	-	-	-	-	-	-	8	-35.72	92.77	3.16	0.02
0.15	-0.12	+	-	-	-	+	0.64	-	0.25	-	-0.30	0.53	-	+	-	-	-	-	12	-27.68	92.92	3.31	0.02
-0.01	0.36	+	-0.33	-	-	-	-	-	0.37	-	-0.17	0.53	-	-	-	-	-	-	10	-32.30	93.39	3.79	0.01
0.09	-0.09	+	-	-	+	-	0.69	-	0.38	-	-0.29	0.53	-	-	-	-	-	-	11	-30.33	93.65	4.05	0.01
-0.18	0.21	+	-0.21	-	-	-	0.34	-	0.40	-	-	0.54	-	-	-	-	-	-	10	-32.46	93.73	4.12	0.01
0.35	0.42	+	-	-	+	+	0.04	-	-	-	-	0.57	-	-	-	+	-	-	11	-30.36	93.73	4.12	0.01
0.10	-0.08	+	-	0.05	-	-	0.64	-	0.37	-	-0.27	0.56	-	-	-	-	-	-	11	-30.37	93.75	4.14	0.01
0.11	-0.07	+	-	-	-	-	0.66	-	0.36	0.02	-0.27	0.54	-	-	-	-	-	-	11	-30.39	93.77	4.16	0.01
0.34	0.63	+	-	-	+	+	-	-	0.36	0.12	-	0.52	-	-	-	-	-	-	11	-30.43	93.86	4.25	0.01
0.25	-0.19	+	-	-	-	+	0.58	-	-	-	-0.32	0.53	-	-	-	+	-	-	11	-30.46	93.92	4.32	0.01
0.26	0.44	+	-	-	+	+	0.14	-	0.25	-	-	0.55	-	-	-	+	-	-	12	-28.19	93.95	4.34	0.01
0.42	0.46	+	-	-	+	-	-	-	0.14	-	-	0.52	-	-	+	-	-	-	10	-32.59	93.97	4.36	0.01
0.06	0.25	+	-	-	-	+	0.43	-	0.43	-	-	0.53	-	-	-	-	-	-	10	-32.63	94.06	4.45	0.01
0.17	0.48	+	-	-	+	+	0.21	-	0.37	-	-	0.56	-	-	-	-	-	-	11	-30.55	94.09	4.49	0.01

Table 1-S7 following. Model without weighting (see Table 1-S10 for output model with weighting). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	Lifespan Effect Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.39	0.59	+	-	-	-	+	-	-	0.42	-	-	0.53	-	-	-	-	-	-	9	-34.70	94.33	4.72	0.01
0.25	0.56	+	-	0.13	+	+	-	-	0.37	-	-	0.60	-	-	-	-	-	-	11	-30.73	94.46	4.85	0.01
-0.15	0.37	+	-0.37	-	-	-	-	-	0.42	0.14	-	0.48	-	-	-	-	-	-	10	-32.85	94.50	4.90	0.01
0.37	0.62	+	-	-	+	+	-	-	0.34	-	-0.07	0.56	-	-	-	-	-	-	11	-30.76	94.53	4.92	0.01

Model set with Δ AICc ≤ 5. N = 22 populations, 21 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models.

Table 1-S8. Justification for the interactions used in the analysis of the Delay Index.

Interaction	Reason for inclusion in the model
Before Variation Index *x* After Variation Index	To test if the relative timing of the Optimal AFR over reproductive lifespan (Delay Index) was influenced simultaneously by a LRS cost from initiating reproduction both before the optimal timing (Before Variation Index) and after the optimal timing (After Variation Index).
Choice Index *x* Before Variation Index	To test if Delay Index was influenced simultaneously by the level of probability to adopt an AFR leading to the highest fitness return (i.e. the span of "beneficial AFR" within the observed range of AFR) and a LRS cost from initiating reproduction before Optimal AFR. *We expect species with a large span of "beneficial AFR" and a low LRS cost of early reproduction to benefit from a late AFR.*
Choice Index *x* After Variation Index	To test if Delay Index was influenced simultaneously by the level of probability to adopt an AFR leading to the highest fitness return (i.e. the span of "beneficial AFR" within the observed range of AFR) and a LRS cost from initiating reproduction after Optimal AFR. *We expect species with a small span of "beneficial AFR" and a high LRS cost of late reproduction to benefit from an early AFR.*
Mean lifespan *x* Family-living	For each of these interactions we tested whether sociality influenced the effect of the focal predictors on Delay Index based on the idea that living in a kin group (Family living) or breeding cooperatively (Helper presence) might buffer costs associated with the timing of the AFR within the reproductive lifespan. *For instance, species with a high risk of nest predation need to get experience to successfully defend their nest and have a greater reproductive output. Consequently, they might benefit from a later AFR. However, if the presence of helpers provides anti-predator protection, it might allow less experienced individuals to still achieve a good reproductive output. Therefore, we expect species with a high risk of nest predation breeding cooperatively to benefit more from an earlier AFR than species with a high risk of nest predation but breeding as a pair without helpers.*
Mean lifespan *x* Helper presence	
Nest predation risk *x* Family-living	
Nest predation risk *x* Helper presence	
Choice Index *x* Family-living	
Choice Index *x* Helper presence	

The variables included in the interactions are explained in the manuscript as well as in Table 1-1 for the indices.

Table 1-S9. Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	Sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.14	0.46	+	-	-	+	+	-	-	0.36	0.22	-	-	-	-	+	+	-	-	-	-	12	-60.84	152.05	0.00	0.05
0.06	0.30	+	-	-0.03	+	+	0.19	-	0.36	0.28	-	-	-	-	-	-	+	+	+	+	16	-54.44	152.97	0.92	0.03
0.06	0.33	+	-	-0.03	+	+	0.17	-	0.37	0.28	-	-	-	-	+	-	+	+	-	+	16	-54.74	153.56	1.51	0.02
0.22	0.47	+	-	-	+	+	-	-	0.47	0.29	-	-	-	0.22	+	+	-	-	-	-	13	-60.14	153.86	1.81	0.02
0.23	0.27	+	-	0.28	-	-	-	-	0.67	0.43	-	-	-	0.52	-	-	-	-	-	-	10	-64.84	153.99	1.94	0.02
0.10	0.22	+	-	-0.04	+	+	0.25	-	0.35	0.30	-0.16	-	-	-	-	-	+	+	+	+	17	-53.12	154.16	2.11	0.02
0.19	0.44	+	-	-	+	+	-	-	0.36	0.22	-0.11	-	-	-	+	+	-	-	-	-	13	-60.30	154.19	2.14	0.02
0.33	0.43	+	-	-	-	-	-	-	0.62	0.39	-	-	-	0.42	-	-	-	-	-	-	9	-66.41	154.29	2.24	0.02
0.10	0.25	+	-	-0.04	+	+	0.24	-	0.37	0.29	-0.17	-	-	-	+	-	+	+	-	+	17	-53.28	154.48	2.43	0.01
0.07	0.36	+	-	-0.02	+	+	0.12	-	0.34	0.27	-	-	-	-	-	-	+	+	-	+	15	-57.10	154.64	2.59	0.01
0.10	0.49	+	-	-	+	+	-	+	0.37	0.23	-	-	-	-	+	+	-	-	-	-	13	-60.60	154.79	2.74	0.01
-0.02	0.40	+	-0.10	-	+	+	-	-	0.38	0.24	-	-	-	-	+	+	-	-	-	-	13	-60.61	154.81	2.76	0.01
0.09	0.50	+	-	-	+	+	-	-	0.35	-	-	-	-	-	+	+	-	-	-	-	11	-63.77	154.82	2.77	0.01
0.08	0.39	+	-	-	+	+	0.09	-	0.37	0.23	-	-	-	-	+	+	-	-	-	-	13	-60.73	155.03	2.98	0.01
0.30	0.22	+	-	0.32	-	-	-	-	0.69	0.46	-0.15	-	-	0.57	-	-	-	-	-	-	11	-63.89	155.06	3.01	0.01
0.06	0.32	+	-	-0.03	+	+	0.17	-	0.37	0.29	-	-	-	-	-	+	+	+	-	+	16	-55.49	155.06	3.01	0.01
0.13	0.45	+	-	0.02	+	+	-	-	0.37	0.22	-	-	-	-	+	+	-	-	-	-	13	-60.83	155.25	3.20	0.01
0.15	0.29	+	-	0.03	+	+	0.14	-	0.46	0.35	-	-	-	0.23	-	-	+	+	+	+	17	-53.73	155.38	3.33	0.01
0.05	0.23	+	-	0.03	+	+	0.22	+	0.36	0.33	-0.22	-	-	-	-	-	+	+	+	+	18	-51.82	155.55	3.50	0.01
0.05	0.28	+	-	-0.03	+	+	0.21	-	0.38	0.29	-	-	-	-	-	+	+	+	+	+	17	-53.84	155.60	3.55	0.01
0.30	0.44	+	-	-	+	+	-	-	0.47	0.31	-0.13	-	-	0.25	+	+	-	-	-	-	14	-59.38	155.69	3.64	0.01

Table 1-S9 following. Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	Sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.10	0.23	+	-	-0.04	+	+	0.25	-	0.37	0.30	-0.17	-	-	-	-	+	+	+	-	+	17	-54.01	155.92	3.87	0.01
0.22	0.20	+	-	0.04	+	+	0.21	-	0.48	0.38	-0.18	-	-	0.28	-	-	+	+	+	+	18	-52.01	155.93	3.88	0.01
0.06	0.30	+	-	-0.03	+	+	0.19	-	0.37	0.28	-	-	-	-	+	-	+	+	+	+	17	-54.04	155.99	3.94	0.01
0.11	0.29	+	-	-0.03	+	+	0.19	-	0.33	0.28	-0.15	-	-	-	-	-	+	+	-	+	16	-55.97	156.03	3.98	0.01
0.02	0.32	+	-	0.01	+	+	0.16	+	0.36	0.30	-	-	-	-	-	-	+	+	+	+	17	-54.06	156.03	3.98	0.01
0.44	0.35	+	-	-	-	-	-	+	0.65	0.40	-	-	-	0.48	-	-	-	-	-	-	10	-65.86	156.04	3.99	0.01
0.15	0.32	+	-	0.03	+	+	0.12	-	0.47	0.35	-	-	-	0.22	+	-	+	+	-	+	17	-54.07	156.05	4.00	0.01
0.10	0.39	+	-	-	+	+	0.07	-	0.37	0.22	-	-	-	-	+	+	+	-	-	-	14	-59.66	156.25	4.20	0.01
0.39	0.42	+	-	-	-	-	-	-	0.63	0.40	-0.11	-	-	0.44	-	-	-	-	-	-	10	-65.98	156.27	4.22	0.01
0.22	0.22	+	-	0.03	+	+	0.19	-	0.49	0.38	-0.19	-	-	0.28	+	-	+	+	-	+	18	-52.21	156.33	4.28	0.01
0.06	0.26	+	-	0.02	+	+	0.21	+	0.37	0.33	-0.22	-	-	-	+	-	+	+	-	+	18	-52.22	156.34	4.29	0.01
0.10	0.39	+	-0.13	-	-	-	-	-	0.63	0.41	-	-	-	0.42	-	-	-	-	-	-	10	-66.04	156.38	4.33	0.01
0.18	0.35	+	-	0.05	+	+	0.07	-	0.46	0.35	-	-	-	0.27	-	-	+	+	-	+	16	-56.16	156.41	4.36	0.01
0.16	0.48	+	-	-	+	+	-	+	0.36	0.24	-0.14	-	-	-	+	+	-	-	-	-	14	-59.74	156.42	4.37	0.01
0.25	0.20	+	-	0.05	+	+	0.20	-	0.53	0.42	-0.20	-	-	0.35	-	+	+	+	-	+	18	-52.32	156.54	4.49	0.01
-0.02	0.34	+	-0.15	-	+	+	-	-	0.38	0.25	-0.14	-	-	-	+	+	-	-	-	-	14	-59.81	156.57	4.52	0.01
0.09	0.20	+	-	-0.04	+	+	0.28	-	0.37	0.31	-0.17	-	-	-	-	+	+	+	+	+	18	-52.33	156.58	4.53	0.00
0.05	0.40	+	-0.11	-	+	+	-	-	0.48	0.31	-	-	-	0.22	+	+	-	-	-	-	14	-59.86	156.66	4.61	0.00
0.18	0.30	+	-	0.05	+	+	0.12	-	0.50	0.38	-	-	-	0.29	-	+	+	+	-	+	17	-54.38	156.67	4.62	0.00
0.30	0.24	+	-	0.25	-	-	-	+	0.68	0.43	-	-	-	0.55	-	-	-	-	-	-	11	-64.70	156.67	4.62	0.00
0.18	0.42	+	-	-	-	-	-	-	0.43	0.25	-	-	-	-	-	-	-	-	-	-	8	-68.98	156.67	4.62	0.00
0.20	0.41	+	-	0.10	+	+	-	-	0.49	0.32	-	-	-	0.27	+	+	-	-	-	-	14	-59.91	156.76	4.71	0.00

Table 1-S9 following. Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	Sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.09	0.30	+	0.03	-0.03	+	+	0.20	-	0.36	0.28	-	-	-	-	-	-	+	+	+	+	17	-54.43	156.76	4.71	0.00
0.30	0.31	+	-	0.32	-	-	-0.09	-	0.66	0.44	-	-	-	0.53	-	-	-	-	-	-	11	-64.74	156.77	4.72	0.00
0.13	0.26	+	-0.06	0.26	-	-	-	-	0.67	0.44	-	-	-	0.52	-	-	-	-	-	-	11	-64.75	156.77	4.72	0.00
0.19	0.44	+	-	-	+	+	-	-	0.36	0.17	-0.14	0.06	-	-	+	+	-	-	-	-	14	-59.94	156.82	4.77	0.00
0.04	0.35	+	-	0.00	+	+	0.15	+	0.37	0.29	-	-	-	-	+	-	+	+	-	+	17	-54.49	156.89	4.84	0.00
0.16	0.38	+	-	-	+	+	0.10	-	0.48	0.30	-	-	-	0.22	+	+	-	-	-	-	14	-59.98	156.90	4.85	0.00
0.25	0.37	+	-	-	-	-	0.09	-	0.63	0.39	-	-	-	0.42	-	-	-	-	-	-	10	-66.30	156.91	4.86	0.00
0.23	0.27	+	-	0.28	-	+	-	-	0.67	0.44	-	-	-	0.52	-	-	-	-	-	-	11	-64.83	156.93	4.88	0.00
0.24	0.27	+	-	0.28	+	-	-	-	0.67	0.44	-	-	-	0.52	-	-	-	-	-	-	11	-64.83	156.95	4.90	0.00
0.11	0.32	+	-	-	+	+	0.14	-	0.37	0.23	-0.13	-	-	-	+	+	-	-	-	-	14	-60.03	157.00	4.95	0.00

Model set with Δ AICc ≤ 5. N = 36 populations, 34 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models.

Table 1-S10. Model selection output for the analysis of Delay Index variation including Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	Lifespan Effect Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.36	0.05	+	-	-	-	-	0.53	-	0.36	-	-0.33	0.53	-	-	-	-	-	-	10	-24.97	78.73	0.00	0.10
0.42	0.61	+	-	-	+	+	-	-	0.35	-	-	0.53	-	-	-	-	-	-	10	-25.55	79.90	1.17	0.06
0.35	0.30	+	-	0.39	-	-	-	+	0.38	-	-0.36	0.61	-	-	-	-	-	-	11	-23.91	80.82	2.09	0.04
0.51	0.58	+	-	-	+	+	-	-	0.33	-	-0.19	0.52	-	-	-	-	-	-	11	-23.91	80.82	2.09	0.04
0.35	0.08	+	-	-	-	+	0.53	-	0.38	-	-0.32	0.51	-	-	-	-	-	-	11	-24.30	81.61	2.87	0.02
0.68	0.78	+	0.21	-	+	+	-	-	0.31	-	-	0.54	-	-	-	-	-	-	11	-24.39	81.78	3.05	0.02
0.41	0.16	+	-	-	-	-	0.43	+	0.35	-	-0.36	0.52	-	-	-	-	-	-	11	-24.42	81.85	3.11	0.02
0.28	0.00	+	-	0.18	-	-	0.46	-	0.38	-	-0.33	0.57	-	-	-	-	-	-	11	-24.48	81.97	3.23	0.02
0.60	0.55	+	-	-	-	-	-	+	0.32	-	-0.33	0.54	-	-	-	-	-	-	10	-26.64	82.09	3.36	0.02
0.41	0.59	+	-	-	+	+	-	-	0.31	-	-	0.51	-	-	+	-	-	-	11	-24.69	82.38	3.65	0.02
0.42	0.59	+	-	-	+	+	-	-	0.31	-	-	0.52	-	+	-	-	-	-	11	-24.70	82.41	3.68	0.02
0.29	0.24	+	-	-	-	-	0.37	-	0.38	-	-	0.56	-	-	-	-	-	-	9	-28.90	82.72	3.98	0.01
0.33	-0.01	+	-	-	+	-	0.60	-	0.37	-	-0.35	0.52	-	-	-	-	-	-	11	-24.88	82.76	4.03	0.01
0.33	0.37	+	-0.21	-	-	-	-	-	0.35	-	-0.28	0.55	-	-	-	-	-	-	10	-27.02	82.83	4.10	0.01
0.35	0.04	+	-	-	-	-	0.54	-	0.36	0.02	-0.33	0.52	-	-	-	-	-	-	11	-24.95	82.90	4.17	0.01
0.37	0.04	+	0.02	-	-	-	0.56	-	0.36	-	-0.33	0.53	-	-	-	-	-	-	11	-24.96	82.91	4.18	0.01
0.75	0.80	+	0.28	-	+	+	-	-	0.24	-	-	0.51	-	-	+	-	-	-	12	-22.69	82.94	4.20	0.01
0.41	0.61	+	-	-	+	+	-	-	0.35	0.11	-	0.52	-	-	-	-	-	-	11	-25.04	83.07	4.34	0.01
0.48	0.55	+	-	-	-	-	-	-	0.35	-	-	0.59	-	-	-	-	-	-	8	-30.90	83.14	4.41	0.01
0.33	0.33	+	-	0.40	-	+	-	+	0.41	-	-0.36	0.58	-	-	-	-	-	-	12	-22.80	83.17	4.44	0.01

Table 1-S10 following. Model selection output for the analysis of Delay Index variation including Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	Lifespan Effect Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.50	0.56	+	-	-	+	+	-	-	0.29	-	-0.20	0.50	-	-	+	-	-	-	12	-22.84	83.24	4.51	0.01
0.29	0.26	+	-	0.45	-	-	-	+	0.39	0.17	-0.38	0.59	-	-	-	-	-	-	12	-22.84	83.25	4.52	0.01
0.75	0.78	+	0.27	-	+	+	-	-	0.25	-	-	0.53	-	+	-	-	-	-	12	-22.85	83.26	4.53	0.01
0.51	0.55	+	-	-	+	+	-	-	0.29	-	-0.19	0.52	-	+	-	-	-	-	12	-22.89	83.35	4.62	0.01
0.35	0.27	+	-	0.37	-	-	-	-	0.38	-	-0.24	0.65	-	-	-	-	-	-	10	-27.28	83.37	4.64	0.01
0.52	0.80	+	-	-	+	+	-0.21	-	0.33	-	-	0.54	-	-	-	-	-	-	11	-25.27	83.53	4.80	0.01
0.34	0.53	+	-	0.13	+	+	-	-	0.37	-	-	0.56	-	-	-	-	-	-	11	-25.31	83.61	4.88	0.01
0.58	0.52	+	-	-	-	-	-	-	0.33	-	-0.21	0.58	-	-	-	-	-	-	9	-29.39	83.69	4.96	0.01

Model set with Δ $AIC_c \leq 5$. N = 22 populations, 21 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models

Table 1-S11. Results from models testing the within- and among-species effect of AFR on LRS (N = 36 populations, 34 species). Estimates and 95% confidence intervals (CI) are presented. Δ AICc corresponds to the change in AICc when the specific parameter was included vs. excluded from the full model.

		Standard deviation	Estimate	95% CI	Δ AIC_c
Fixed effects:					
intercept			-0.12	(-0.87, 0.62)	-
ln(body mass)*			-0.11	(-0.29, 0.08)	0.91
sex	Both		0.00	na	3.09
	Female		0.38	(-0.37, 1.14)	
	Male		0.41	(-0.34, 1.16)	
within-species AFR*			-0.54	(-0.70, -0.39)	-43.83†
within-species AFR^2*			-0.26	(-0.43, -0.10)	-7.45†
between-species AFR			0.08	(-0.13, 0.29)	1.57
Random effects:					
species		0.00		(0.00, 0.16)	
residuals		19.64		(18.14, 21.35)	

* factor centered and scaled; na – not applicable; † support for inclusion of the factor

Table 1-S12. Correlation between Optimal AFR vs. modal AFR and Optimal AFR vs. mean AFR.

cases	Mean AFR vs. Optimal AFR			AFR mode vs. Optimal AFR		
	Correlation coefficient	**P**	**Slope**	**Correlation coefficient**	**P**	**Slope**
all (N=62)	0.84 (Spearman)	< 0.0001	0.95	0.80 (Spearman)	< 0.0001	0.98
with AFR range > 4 (N=29)	0.85 (Spearman)	< 0.0001	0.99	0.87 (Spearman)	< 0.0001	0.82
with AFR range > 6 (N=12)	0.96 (Pearson)	< 0.0001	1.13	0.92 (Pearson)	< 0.0001	1.06

Table 1-S13. Model with 90CI indices (see Table 1-3 for comparison). Relative importance of predictors included in the full model for the analysis of Delay Index variation excluding Lifespan Effect Index (N = 36 populations, 34 species) and model averaging estimates (based on 51 models with Δ AICc ($AICc_{focal\ model} - AICc_{best\ model}$) ≤ 5, see Table 1-S15).

Predictors	**Predictor weight***	**Relative importance of predictors†**	**Model averaging estimates‡,§**	**95% CI**
Intercept			0.42	(-0.60, 1.44)
ln(body mass)	0.51	1.00	0.21	(-0.17, 0.59)
Sex	0.51	1.00	Both: 0.00 Female: -0.30 Male: -0.54	na (-1.40, 0.79) (-1.64, 0.56)
Choice Index 90CI ¶	0.51	1.00	0.53	(0.29, 0.77)
Before Variation Index 90CI ¶	0.51	1.00	0.36	(-0.02, 0.74)
Before Variation Index 90CI: Choice Index 90CI	0.51	1.00	0.86	(0.35, 1.37)
nest predation risk	0.41	0.80	0.35	(0.03, 0.84)
After Variation Index 90CI ¶	0.35	0.69	-0.17	(-0.49, 0.01)
Before Variation Index 90CI: After Variation Index 90CI	0.17	0.33	-0.05	(-0.32, 0.01)
family-living	0.13	0.26	NO: 0.00 YES: 0.15	na (-0.95, 2.15)
chick development mode	0.12	0.24	Altricial: 0.00 Precocial: 0.17	na (-0.28, 1.69)
mean lifespan	0.10	0.20	-0.04	(-0.77, 0.35)
helper presence	0.10	0.19	NO: 0.00 YES: -0.12	na (-2.91, 1.63)
nest predation risk: family-living	0.05	0.09	NO: 0.00 YES: 0.09	na (-0.34, 2.21)
Choice Index: helper presence	0.04	0.08	NO: 0.00 YES: -0.12	na (-2.55, -0.30)
latitude	0.04	0.08	0.00	(-0.30, 0.42)
Choice Index: family-living	0.04	0.07	NO: 0.00 YES: 0.11	na (0.62, 2.44)
After Variation Index 90CI: Choice Index 90CI	0.02	0.04	-0.00	(-0.53, 0.48)
mean lifespan: helper presence	0.02	0.03	NO: 0.00 YES: 0.13	na (2.18, 7.04)
mean lifespan: family-living	0.02	0.03	NO: 0.00 YES: -0.10	na (-5.17, -1.96)
nest predation risk: helper presence	0.01	0.01	NO: 0.00 YES: -0.01	na (-3.41, 0.27)

*: sum of model weights from Table 1-S15 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.05) (Symonds & Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS and AFR, see Table 1-1 and the Indices and estimates section of Materials and methods.

Table 1-S14. Model with 90CI indices (see Table 1-4 for comparison). Relative importance of predictors included in the full model for the analysis of Delay Index variation including Lifespan Effect Index (N = 22 populations, 21 species) and model averaging estimates (based on 45 models with Δ AICc ($AICc_{focal\ model} - AICc_{best\ model}$) ≤ 5, see Table 1-S16).

Predictors	Predictor weight*	Relative importance of predictors†	Model averaging estimates‡,§	95% CI
intercept			0.64	(-0.24, 1.52)
ln(body mass)	0.61	1.00	0.47	(-0.02, 0.96)
Sex	0.61	1.00	Both: 0.00	na
			Female: -0.82	(-1.51, 0.34)
			Male: -0.59	(-1.52, 0.34)
Lifespan Effect Index ¶	0.61	1.00	0.47	(0.25, 0.69)
Choice Index 90CI ¶	0.58	0.96	0.34	(0.11, 0.61)
Before Variation Index 90CI ¶	0.32	0.52	0.12	(-0.09, 0.56)
Before Variation Index 90CI: Choice Index 90CI	0.31	0.51	0.25	(0.18, 0.83)
After Variation Index 90CI ¶	0.29	0.47	-0.12	(-0.51, -0.01)
family-living	0.16	0.27	NO: 0.00	na
			YES: -0.25	(-2.30, 0.45)
nest predation risk	0.15	0.25	0.10	(-0.01, 0.82)
helper presence	0.15	0.25	NO: 0.00	na
			YES: 0.42	(-1.19, 4.58)
chick development mode	0.09	0.15	Altricial: 0.00	na
			Precocial: -0.08	(-1.27, 0.18)
mean lifespan	0.08	0.14	-0.02	(-0.94, 0.71)
Latitude	0.08	0.14	0.03	(-0.33, 0.70)
Mean lifespan: helper presence	0.04	0.06	NO: 0.00	na
			YES: 0.20	(-0.44, 7.34)
Choice Index: helper presence	0.01	0.02	NO: 0.00	na
			YES: -0.03	(-2.45, -0.28)
Choice Index: family-living	0.01	0.02	NO: 0.00	na
			YES: 0.01	(-0.11, 0.80)

*: sum of model weights from Table 1-S16 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.06) (Symonds & Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS or survival and AFR, see Table 1-1 and the Indices and estimates section of Materials and methods.

Table 1-S15. Model with 90CI indices (see Table 1-S9 for comparison). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	Sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	After Variation Index 90CI : Before Variation Index 90CI	After Variation Index 90CI : Choice Index 90CI	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.27	0.16	+	-	0.44	-	-	-	-	0.52	0.31	-0.25	-	-	0.81	-	-	-	-	-	-	11	-67.68	162.63	0.00	0.04
0.32	0.13	+	-	0.49	-	-	-	-	0.59	0.56	-0.25	-0.14	-	1.03	-	-	-	-	-	-	12	-66.22	162.80	0.17	0.04
0.22	0.25	+	-	0.35	-	-	-	-	0.47	0.23	-	-	-	0.71	-	-	-	-	-	-	10	-69.72	163.76	1.12	0.02
0.57	0.29	+	-	0.62	-	-	-0.33	-	0.61	0.60	-0.23	-0.17	-	1.11	-	-	-	-	-	-	13	-65.15	163.89	1.26	0.02
0.63	0.29	+	-	-	-	-	-	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	10	-69.83	163.98	1.34	0.02
0.47	0.18	+	-	0.27	-	-	-	+	0.51	0.21	-	-	-	0.80	-	-	-	-	-	-	11	-68.66	164.61	1.97	0.02
0.44	0.27	+	-	0.53	-	-	-0.23	-	0.52	0.30	-0.24	-	-	0.83	-	-	-	-	-	-	12	-67.19	164.74	2.11	0.02
0.50	0.09	+	-	0.36	+	-	-	-	0.55	0.29	-0.27	-	-	0.88	-	-	-	-	-	+	13	-65.61	164.81	2.17	0.01
0.42	0.12	+	-	0.37	-	-	-	+	0.53	0.29	-0.22	-	-	0.85	-	-	-	-	-	-	12	-67.26	164.88	2.24	0.01
0.48	0.09	+	-	0.41	-	-	-	+	0.61	0.54	-0.21	-0.15	-	1.09	-	-	-	-	-	-	13	-65.68	164.94	2.30	0.01
0.35	0.45	+	-	-	-	-	-	-	0.43	0.22	-	-	-	0.62	-	-	-	-	-	-	9	-71.77	165.01	2.37	0.01
0.46	0.17	+	0.11	0.48	-	-	-	-	0.53	0.31	-0.25	-	-	0.83	-	-	-	-	-	-	12	-67.46	165.29	2.65	0.01
0.43	0.38	+	-	0.46	-	-	-0.28	-	0.48	0.23	-	-	-	0.75	-	-	-	-	-	-	11	-69.01	165.29	2.66	0.01
0.29	0.14	+	-	0.45	+	-	-	-	0.53	0.32	-0.26	-	-	0.82	-	-	-	-	-	-	12	-67.49	165.34	2.71	0.01
0.53	0.07	+	-	0.41	+	-	-	-	0.61	0.53	-0.27	-0.14	-	1.09	-	-	-	-	-	+	14	-64.27	165.47	2.84	0.01
0.51	0.14	+	0.11	0.52	-	-	-	-	0.60	0.56	-0.25	-0.15	-	1.05	-	-	-	-	-	-	13	-65.97	165.52	2.89	0.01
0.29	0.15	+	-	0.44	-	+	-	-	0.52	0.31	-0.25	-	-	0.81	-	-	-	-	-	-	12	-67.60	165.56	2.93	0.01
0.34	0.11	+	-	0.50	+	-	-	-	0.60	0.57	-0.26	-0.14	-	1.05	-	-	-	-	-	-	13	-66.02	165.63	3.00	0.01
0.39	0.17	+	-	0.34	+	+	-	-	0.49	0.29	-0.26	-	-	0.77	+	+	-	-	-	-	15	-62.63	165.69	3.06	0.01

Table 1-S15 following. Model with 90CI indices (see Table 1-S9 for comparison). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	Sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	After Variation Index 90CI : Before Variation Index 90CI	After Variation Index 90CI : Choice Index 90CI	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.27	0.15	+	-	0.45	-	-	-	-	0.53	0.32	-0.25	-	-0.03	0.81	-	-	-	-	-	-	12	-67.67	165.71	3.07	0.01
0.33	0.12	+	-	0.49	-	+	-	-	0.59	0.56	-0.25	-0.14	-	1.04	-	-	-	-	-	-	13	-66.13	165.84	3.20	0.01
0.64	0.28	+	-	-	-	-	-	+	0.50	0.24	-0.13	-	-	0.78	-	-	-	-	-	-	11	-69.29	165.86	3.22	0.01
0.41	0.42	+	-	-	-	-	-	-	0.45	0.27	-0.17	-	-	0.67	-	-	-	-	-	-	10	-70.84	166.00	3.36	0.01
0.32	0.13	+	-	0.49	-	-	-	-	0.59	0.56	-0.25	-0.14	-0.02	1.03	-	-	-	-	-	-	13	-66.22	166.01	3.38	0.01
0.37	0.45	+	-	-	+	+	-	-	0.39	0.19	-	-	-	0.57	+	+	-	-	-	-	13	-66.27	166.13	3.49	0.01
0.43	0.27	+	0.11	0.39	-	-	-	-	0.48	0.23	-	-	-	0.73	-	-	-	-	-	-	11	-69.48	166.24	3.61	0.01
0.43	0.14	+	-	0.38	+	+	-	-	0.56	0.53	-0.26	-0.14	-	0.99	+	+	-	-	-	-	16	-61.11	166.31	3.67	0.01
0.28	0.14	+	-	0.17	+	+	0.12	-	0.38	0.31	-0.28	-	-	0.55	-	-	+	+	-	+	17	-59.22	166.34	3.71	0.01
0.44	0.20	+	-	0.27	+	-	-	-	0.50	0.21	-	-	-	0.77	-	-	-	-	-	+	12	-68.02	166.41	3.78	0.01
0.45	0.24	+	-0.11	-	-	-	-	+	0.49	0.20	-	-	-	0.77	-	-	-	-	-	-	11	-69.59	166.47	3.83	0.01
0.24	0.25	+	-	0.35	-	+	-	-	0.47	0.23	-	-	-	0.71	-	-	-	-	-	-	11	-69.66	166.60	3.97	0.01
0.23	0.24	+	-	0.36	+	-	-	-	0.48	0.23	-	-	-	0.72	-	-	-	-	-	-	11	-69.67	166.62	3.98	0.01
0.66	0.24	+	-	0.55	-	-	-0.29	+	0.62	0.58	-0.20	-0.17	-	1.15	-	-	-	-	-	-	14	-64.87	166.68	4.04	0.01
0.42	0.04	+	-	0.47	+	+	-	-	0.56	0.32	-0.29	-	-	0.87	-	-	-	-	-	-	13	-66.60	166.78	4.15	0.01
0.71	0.27	+	-	-	-	-	-	+	0.56	0.45	-0.12	-0.12	-	0.98	-	-	-	-	-	-	12	-68.25	166.88	4.24	0.01
0.45	0.40	+	-	-	+	+	-	-	0.41	0.24	-0.19	-	-	0.62	+	+	-	-	-	-	14	-64.97	166.88	4.25	0.01
0.64	0.29	+	-	-	-	+	-	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	11	-69.80	166.89	4.25	0.01

Table 1-S15 following. Model with 90CI indices (see Table 1-S9 for comparison). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions								Model information				
(Intercept)	ln(body mass)	Sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	After Variation Index 90CI : Before Variation Index 90CI	After Variation Index 90CI : Choice Index 90CI	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Lik	AICc	Δ AICc	weight
0.62	0.28	+	-	-	-	-	0.02	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	11	-69.83	166.94	4.30	0.01
0.63	0.29	+	-	-	+	-	-	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	11	-69.83	166.94	4.31	0.01
0.58	0.28	+	-	0.36	-	-	-0.20	+	0.51	0.21	-	-	-	0.81	-	-	-	-	-	-	12	-68.29	166.96	4.32	0.01
0.30	0.29	+	-	0.24	+	+	-	-	0.43	0.21	-	-	-	0.65	+	+	-	-	-	-	14	-65.01	166.96	4.33	0.01
0.46	0.01	+	-	0.51	+	+	-	-	0.63	0.57	-0.29	-0.15	-	1.10	-	-	-	-	-	-	14	-65.08	167.09	4.45	0.00
0.58	0.28	+	-	0.62	-	+	-0.33	-	0.61	0.60	-0.23	-0.17	-	1.11	-	-	-	-	-	-	14	-65.10	167.14	4.50	0.00
0.56	0.27	+	-	0.62	+	-	-0.32	-	0.61	0.60	-0.23	-0.17	-	1.11	-	-	-	-	-	-	14	-65.13	167.19	4.55	0.00
0.55	0.29	+	-0.01	0.62	-	-	-0.34	-	0.61	0.60	-0.23	-0.18	-	1.11	-	-	-	-	-	-	14	-65.15	167.24	4.60	0.00
0.57	0.29	+	-	0.62	-	-	-0.33	-	0.61	0.60	-0.23	-0.17	-0.01	1.11	-	-	-	-	-	-	14	-65.15	167.24	4.61	0.00
0.54	0.37	+	-	-	+	+	-	+	0.43	0.17	-	-	-	0.68	+	+	-	-	-	-	14	-65.21	167.35	4.72	0.00
0.53	0.22	+	-	0.46	-	-	-0.19	+	0.53	0.29	-0.21	-	-	0.86	-	-	-	-	-	-	13	-66.93	167.44	4.81	0.00
0.26	0.09	+	-	0.16	+	+	0.17	-	0.38	0.31	-0.29	-	-	0.53	-	-	+	+	+	+	18	-57.77	167.45	4.82	0.00
0.45	0.41	+	-	-	-	-	-	-	0.50	0.45	-0.16	-0.11	-	0.83	-	-	-	-	-	-	11	-70.11	167.49	4.86	0.00
0.27	0.14	+	-	0.16	+	+	0.14	-	0.39	0.30	-0.26	-	-	0.52	+	-	+	+	-	+	18	-57.81	167.53	4.89	0.00

Model set with Δ AICc ≤ 5. N = 36 populations, 34 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models.

Table 1-S16. Model with 90CI indices (see Table 1-S10 for comparison). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	Sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	Lifespan Effect Index	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.59	0.22	+	-	0.42	-	-	-	-	0.47	0.32	-0.26	0.44	0.58	-	-	-	-	-	12	-24.05	85.66	0.00	0.06
0.82	0.53	+	-	-	-	-	-	-	0.42	0.17	-	0.40	0.47	-	-	-	-	-	10	-28.54	85.89	0.23	0.05
0.88	0.51	+	-	-	-	-	-	-	0.42	0.17	-0.21	0.41	0.48	-	-	-	-	-	11	-26.67	86.34	0.69	0.04
0.57	0.30	+	-	0.34	-	-	-	-	0.46	0.28	-	0.42	0.54	-	-	-	-	-	11	-27.01	87.02	1.37	0.03
0.51	0.48	+	-	-	-	-	-	-	0.30	-	-	0.55	-	-	-	-	-	-	8	-32.89	87.10	1.45	0.03
0.55	0.50	+	-	-	-	-	-	+	0.30	-	-0.31	0.53	-	-	-	-	-	-	10	-29.21	87.22	1.56	0.03
0.32	0.14	+	-	0.56	-	-	-	+	0.43	0.39	-0.37	0.46	0.47	-	-	-	-	-	13	-22.53	87.60	1.95	0.02
0.45	0.52	+	-	-	+	+	-	-	0.26	-	-	0.50	-	-	-	-	-	-	10	-29.40	87.61	1.95	0.02
0.80	0.76	+	0.29	-	+	+	-	-	0.23	-	-	0.51	-	-	-	-	-	-	11	-27.58	88.15	2.50	0.02
0.57	0.46	+	-	-	-	-	-	-	0.30	-	-0.20	0.56	-	-	-	-	-	-	9	-31.62	88.17	2.52	0.02
0.49	0.48	+	-	-	+	-	-	-	0.26	-	-	0.56	-	-	-	-	-	-	9	-31.64	88.21	2.55	0.02
1.00	0.95	+	0.42	-	+	+	-0.18	-	-	-	-	0.49	-	-	-	+	-	-	12	-25.36	88.29	2.63	0.02
0.50	0.50	+	-	-	+	+	-	-	0.26	-	-0.21	0.51	-	-	-	-	-	-	11	-27.75	88.50	2.84	0.01
0.39	0.13	+	-	-	-	-	0.36	-	0.28	-	-0.28	0.52	-	-	-	-	-	-	10	-29.97	88.74	3.08	0.01
0.68	0.99	+	-	-	+	+	-0.49	-	0.24	-	-	0.52	-	-	-	-	-	-	11	-27.95	88.90	3.25	0.01
0.49	0.51	+	-	-	-	-	-	+	0.30	-	-	0.53	-	-	-	-	-	-	9	-32.08	89.09	3.43	0.01
0.82	0.55	+	-	-	-	+	-	-	0.44	0.16	-	0.38	0.47	-	-	-	-	-	11	-28.06	89.12	3.46	0.01
0.55	0.46	+	-	-	+	-	-	-	0.26	-	-0.21	0.57	-	-	-	-	-	-	10	-30.17	89.14	3.49	0.01
0.40	0.34	+	-	0.24	-	-	-	+	0.32	-	-0.34	0.57	-	-	-	-	-	-	11	-28.28	89.56	3.90	0.01
0.40	0.30	+	-	-	-	-	0.20	-	0.29	-	-	0.53	-	-	-	-	-	-	9	-32.34	89.60	3.95	0.01

Table 1-S16 following. Model with 90CI indices (see Table 1-S10 for comparison). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	Lifespan Effect Index	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.77	0.52	+	-	-	+	-	-	-	0.39	0.18	-	0.41	0.43	-	-	-	-	-	11	-28.33	89.65	4.00	0.01
0.79	0.52	+	-	-	-	-	-	+	0.40	0.19	-0.27	0.41	0.40	-	-	-	-	-	12	-26.07	89.70	4.04	0.01
0.59	0.24	+	-	0.41	-	+	-	-	0.48	0.31	-0.25	0.41	0.58	-	-	-	-	-	13	-23.60	89.74	4.08	0.01
1.01	1.07	+	0.37	-	+	+	-0.29	-	0.14	-	-	0.50	-	+	-	+	-	-	14	-20.90	89.80	4.14	0.01
0.46	0.46	+	-	-	+	-	-	-	0.20	-	-	0.52	-	-	+	-	-	-	10	-30.51	89.82	4.16	0.01
0.38	0.41	+	-0.10	-	-	-	-	-	0.30	-	-	0.53	-	-	-	-	-	-	9	-32.46	89.84	4.19	0.01
0.71	0.43	+	-0.10	-	-	-	-	-	0.41	0.20	-0.24	0.39	0.46	-	-	-	-	-	12	-26.15	89.86	4.20	0.01
0.72	0.31	+	-	-	-	-	0.20	-	0.40	0.19	-0.26	0.40	0.43	-	-	-	-	-	12	-26.15	89.86	4.20	0.01
0.74	0.49	+	-0.05	-	-	-	-	-	0.42	0.18	-	0.40	0.46	-	-	-	-	-	11	-28.44	89.87	4.22	0.01
0.88	0.53	+	-	-	-	+	-	-	0.43	0.17	-0.21	0.39	0.48	-	-	-	-	-	12	-26.19	89.94	4.28	0.01
0.40	0.37	+	-	0.17	-	-	-	-	0.31	-	-	0.58	-	-	-	-	-	-	9	-32.52	89.96	4.31	0.01
0.80	0.50	+	-	-	-	-	0.03	-	0.42	0.17	-	0.40	0.46	-	-	-	-	-	11	-28.53	90.06	4.41	0.01
0.82	0.53	+	-	-	-	-	-	+	0.42	0.17	-	0.40	0.46	-	-	-	-	-	11	-28.54	90.08	4.43	0.01
0.38	0.36	+	-0.14	-	-	-	-	-	0.29	-	-0.24	0.54	-	-	-	-	-	-	10	-30.66	90.12	4.46	0.01
0.51	0.50	+	-	-	-	+	-	-	0.31	-	-	0.53	-	-	-	-	-	-	9	-32.62	90.16	4.51	0.01
0.71	1.09	+	-	-	+	+	-0.61	-	0.20	-	-	0.50	-	+	-	+	-	-	13	-23.81	90.17	4.51	0.01
0.64	0.97	+	-	-	+	+	-0.58	-	-	-	-	0.48	-	-	-	+	-	-	11	-28.64	90.28	4.62	0.01

Table 1-S16 following. Model with 90CI indices (see Table 1-S10 for comparison). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	Lifespan Effect Index	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.86	0.79	+	0.35	-	+	+	-	-	0.16	-	-	0.50	-	-	+	-	-	-	12	-26.36	90.28	4.63	0.01
0.83	0.50	+	-	-	+	-	-	-	0.39	0.18	-0.22	0.42	0.44	-	-	-	-	-	12	-26.38	90.33	4.67	0.01
0.52	0.19	+	-0.05	0.40	-	-	-	-	0.46	0.32	-0.27	0.43	0.56	-	-	-	-	-	13	-23.91	90.37	4.72	0.01
0.57	0.49	+	-	-	-	-	-	-	0.30	-0.06	-	0.56	-	-	-	-	-	-	9	-32.75	90.42	4.76	0.01
0.84	0.74	+	0.37	-	+	+	-	-	-	-	-	0.48	-	-	-	-	-	-	10	-30.87	90.53	4.88	0.01
0.60	0.23	+	-	0.43	-	-	-0.02	-	0.47	0.32	-0.25	0.44	0.58	-	-	-	-	-	13	-24.04	90.62	4.97	0.01
0.59	0.22	+	-	0.42	+	-	-	-	0.47	0.32	-0.26	0.44	0.57	-	-	-	-	-	13	-24.04	90.64	4.98	0.00
0.54	0.52	+	-	-	-	+	-	+	0.31	-	-0.31	0.51	-	-	-	-	-	-	11	-28.83	90.65	5.00	0.00

Model set with Δ AICc ≤ 5. N = 22 populations, 21 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models.

Figure 1-S1. Phylogenetic tree for the 34 species studied in this paper (based on the full tree from Jetz *et al.* 2012; Ericson backbone phylogeny).

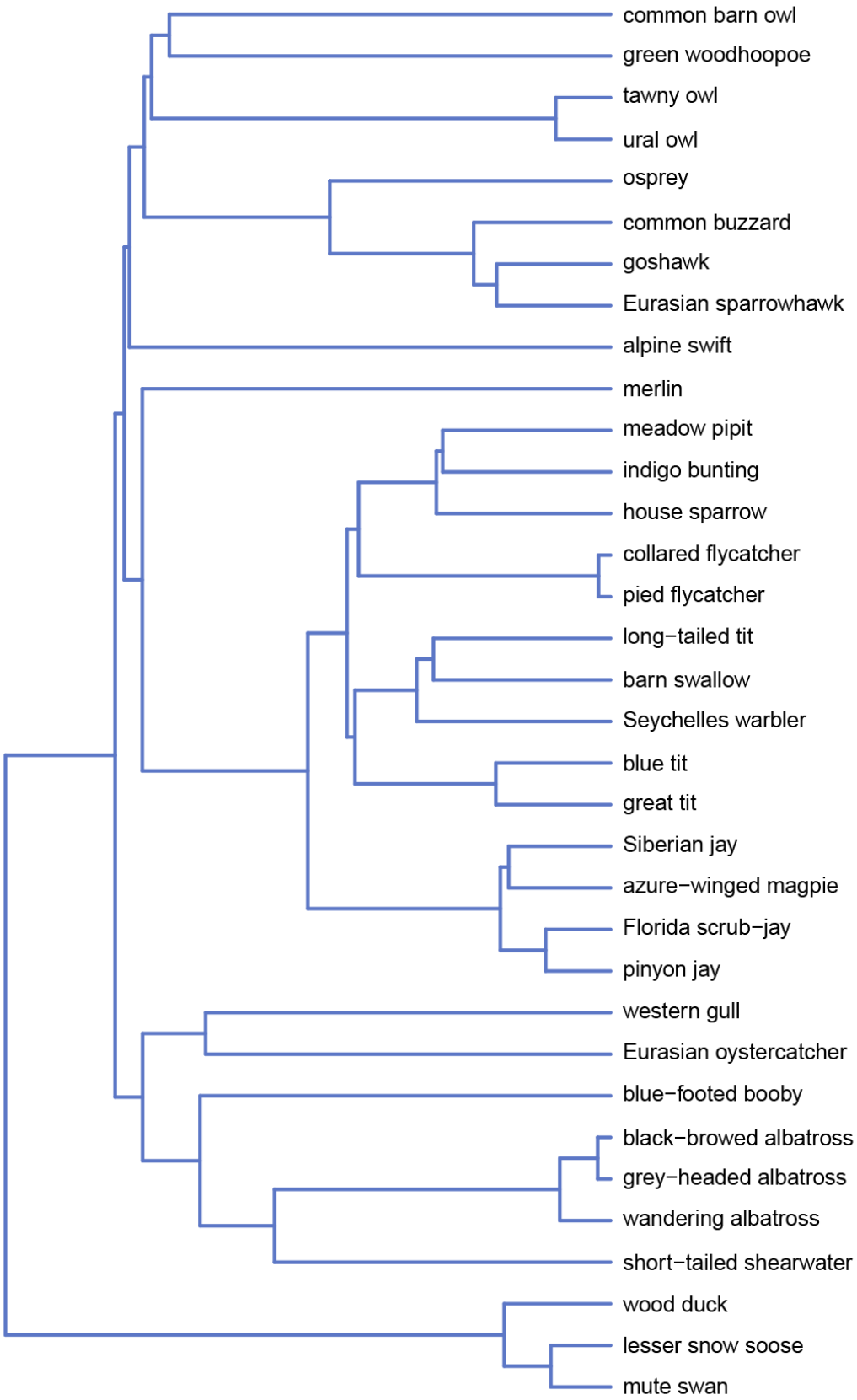


Figure 1-S2. Variation in AFR and consequences for mean reproductive lifespan. Relationship between mean reproductive lifespan (mean lifespan (per AFR classes) minus AFR) and AFR for 22 populations (21 species) used to estimate the Lifespan Effect Index (Table 1-1); each point represents the mean value for individuals that start to reproduce at a specific AFR. B = both sexes, F = female, M = male.

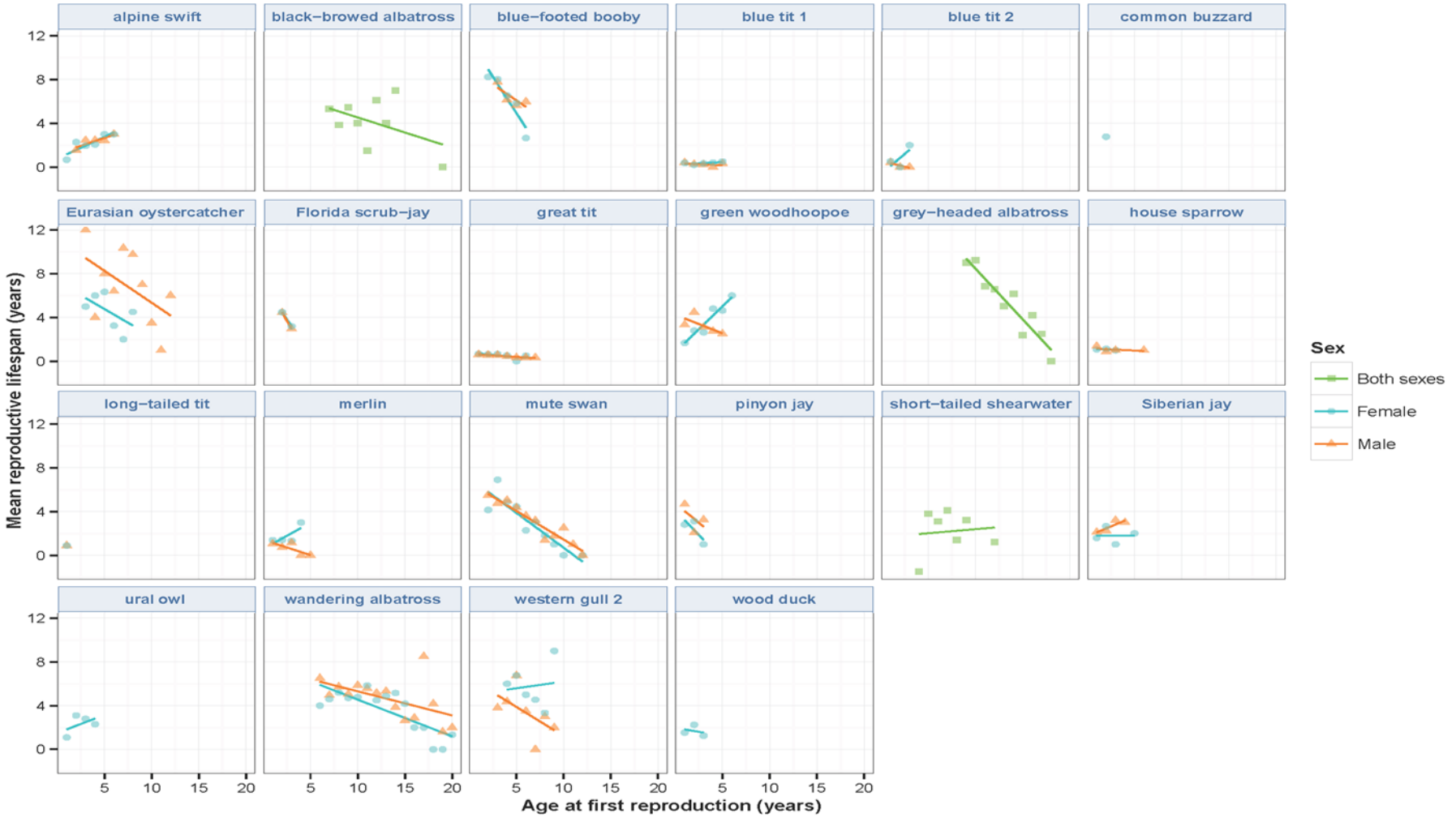
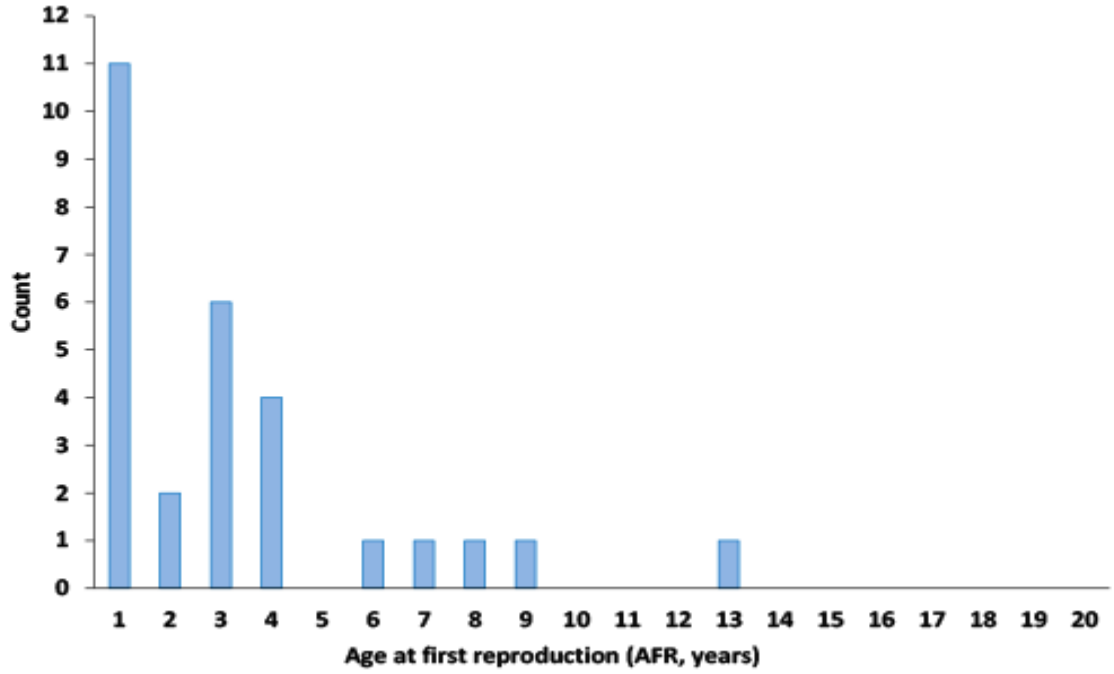


Figure 1-S3. Variation in AFR. **(a)** Number of times the specific AFR corresponded to a species modal AFR (over 28 out of 34 species as we excluded 4 species with only 1 AFR age class and 2 species for which the sample size per AFR age class was missing). **(a)** Frequency of observation of a specific AFR age class across all 34 species (an AFR age-class was counted as being observed within a population when at least one individual initiated reproduction at the focal AFR – e.g. a values of about 20% for an AFR of 9 means that about 7 species (20% of 34) had individuals that initiated their reproduction at age 9).

a)



b)

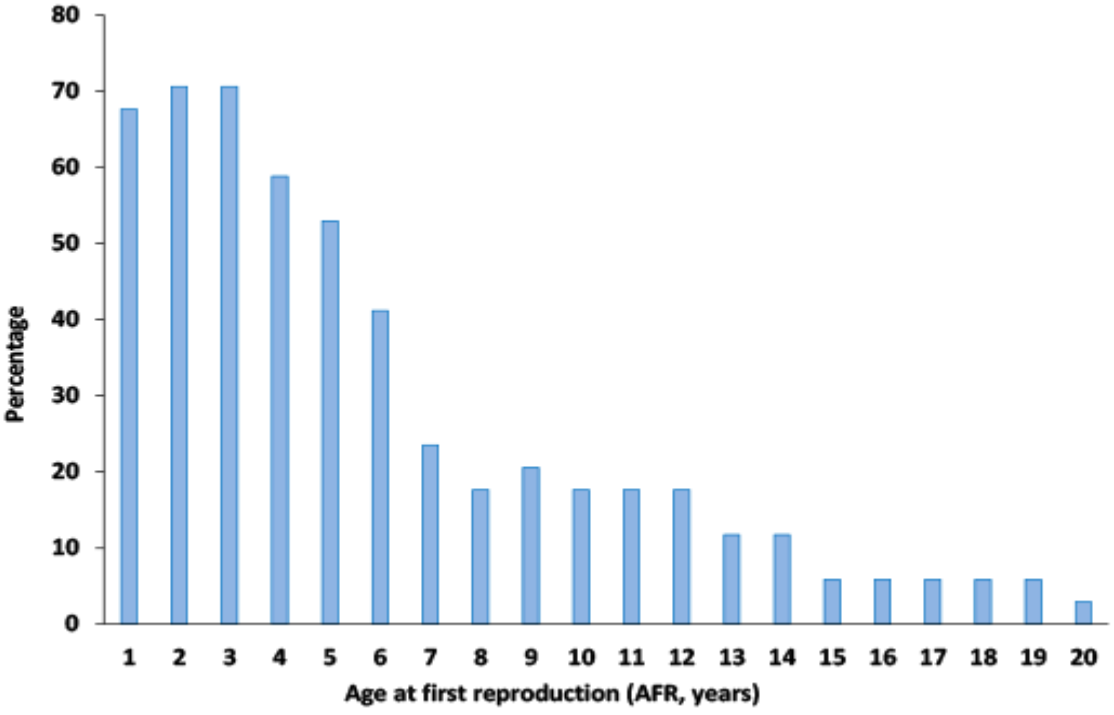
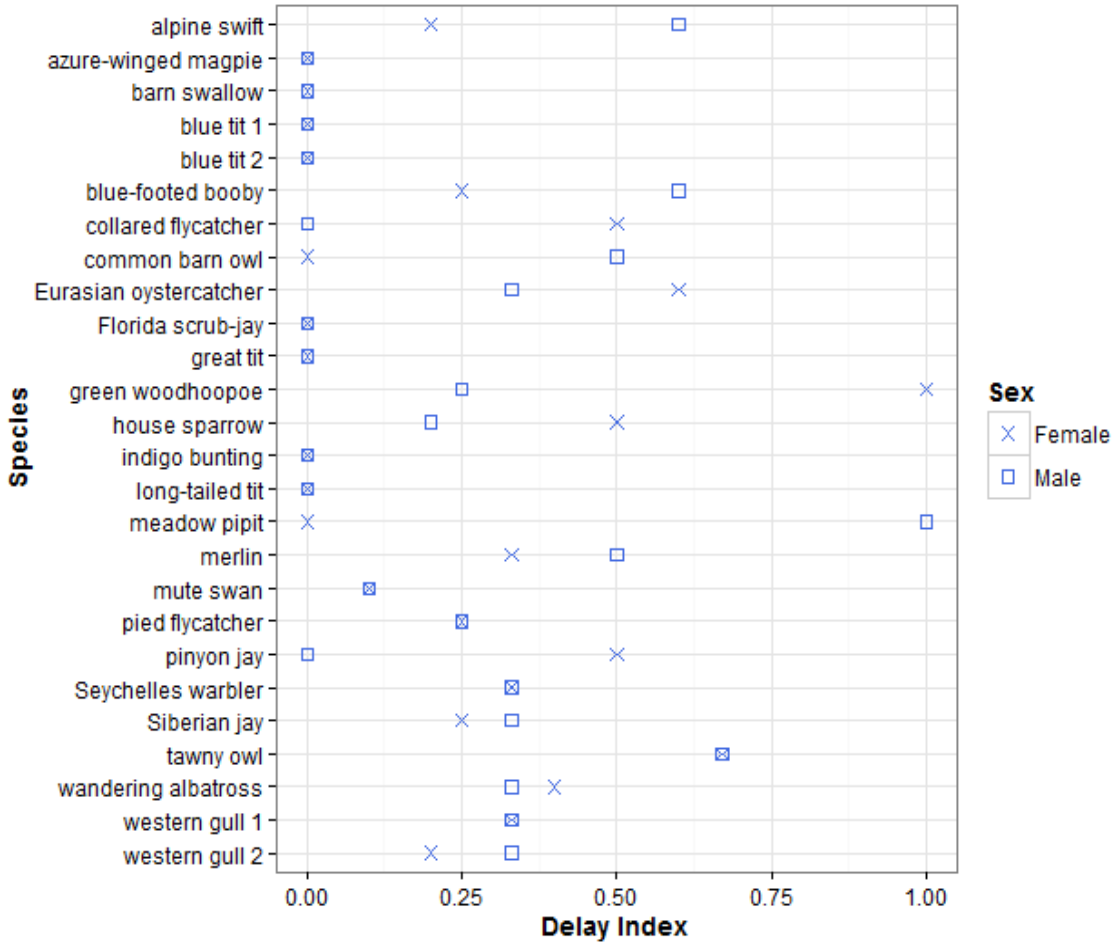


Figure 1-S4. Sex differences in the Delay Index for the 26 populations (24 species) for which we had separate data for males (M, square symbols) and females (F, cross symbols). A number after the species indicates separate studies.



- Chapter 2 -

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Parental care decisions under increased risk of predation to adults or nestlings in 12 altricial bird species

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Abstract

A central issue in life-history theory is the trade-off between survival and reproduction. Predation on adults directly affects the parents' survival and may indirectly affect nestling survival, while predation on nestlings affects their reproductive success only. Hence, parents may respond differently to risk to themselves versus their nestlings, but these responses vary among species and this variation is poorly understood. In this comparative study, we consecutively exposed nests of 12 altricial bird species to a predator representing a risk to i) adults, ii) nestlings and iii) a control non-predatory species, within a given day. We assessed the change in nest visitation rate relative to the change in the control treatment and investigated how this was affected by life-history (lifespan), ecology (re-nesting potential, nest type, nest predation rate), and social factors (post-fledging parent-offspring association time) by using a model selection and averaging approach. Comparing the change in relative nest visitation rate revealed that species decreased their nest visitation rates only in the presence of a predator of adults but not a nestling predator, contrary to expectation. This difference was not influenced by any of the predictors assessed. However, after controlling for the effect of predator type, the reduction in nest visitation rate was stronger in species that do not re-nest within breeding seasons, have a short lifespan, or have open nests. An analysis assessing the response to the presence of predators on adults only, revealed that the reduction of the nest visitation rate was associated with a low re-nesting potential. Overall, this comparative study shows that parental care decisions in response to varying predation risk are critically affected by the probability of re-nesting within the breeding season and within the life of a parent. These results contribute to a better understanding of the evolution of parental care strategies in general.

Key Words: brood value, cost-benefit balance, nestling provisioning, phenotypic plasticity, reproductive investment, reproductive costs

2.1 Introduction

Life-history theory predicts that parents trade off survival against reproduction (Roff 1992; Stearns 1992), but we only vaguely know which factors influence the balance of this trade-off across species (but see Ghalambor & Martin 2000; Ghalambor & Martin 2001). A higher nest visitation rate increases offspring fitness (Scheuerlein & Gwinner 2006; Thomson *et al.* 2006; Lima 2009) and reduces nestling begging, which may attract predators (Budden & Wright 2001; Haff & Magrath 2011). However, it may increase the predation risk to parents (Tye 1984; Clark & Ydenberg 1990; Scheuerlein & Gwinner 2006) or offspring (Skutch 1949; Martin, Scott & Menge 2000) (Figure 2-1). Thus, the presence of a predator near a nest confronts parents with the decision to maintain or change their nest visitation rate.

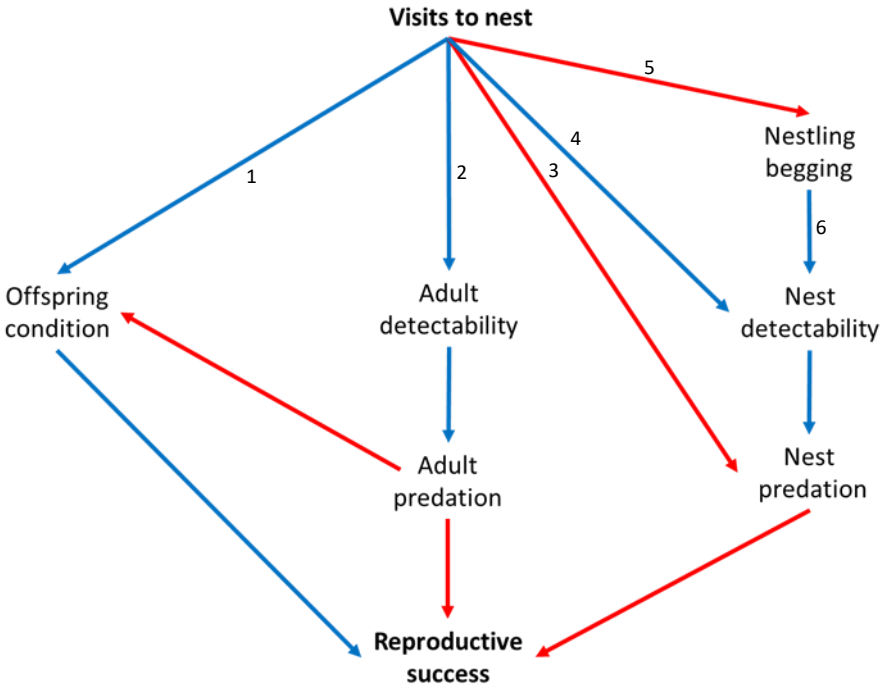

Figure 2-1. Influences of the number of visit to the nest on the reproductive success of the breeding parents seen as a motor for their behavioural decision-making under a risk of predation. The style of the arrow represents the direction of the correlation between two components of the network: red line for negative, blue line for positive.
[1](Scheuerlein & Gwinner 2006; Thomson et al. 2006; Lima 2009), [2](Tye 1984; Scheuerlein & Gwinner 2006), [3](Montgomerie & Weatherhead 1988; Martin & Li 1992; Martin & Ghalambor 1999) , [4](Skutch 1949; Martin, Scott & Menge 2000) , [5](Budden & Wright 2001; Leonard & Horn 2001; Maurer et al. 2003), [6](Redondo & Castro 1992; Leech & Leonard 1997; Briskie, Martin & Martin 1999; Haff & Magrath 2011).

A widespread antipredator adaptation is to reduce the nest visitation rate (Eggers, Griesser & Ekman 2005; Fontaine & Martin 2006; Martin & Briskie 2009; Zanette *et al.* 2011; Ghalambor, Peluc & Martin 2013; Grunst, Grunst & Rotenberry 2015). However, parents may reduce nest visitation rates differently in response to nestling predators and predators of adults (Ghalambor & Martin 2001; Lima 2009) as the consequences on fitness components may differ (Dale, Gustavsen & Slagsvold 1996). While nestling predators only affect the survival of offspring, predators of adults can affect the survival of the parents directly, and nestling condition and survival indirectly through the death of a parent or a reduced nest visitation rate (Figure 2-2). Thus, assessing the response of parents to both a predator of adults and a nest predator, or to a predator of adults only, may give insight into the trade-off between survival and reproduction. However, studies examining parental investment responses to adult predation or different types of predation risk are rare (Dale, Gustavsen & Slagsvold 1996; Lima 2009; Tilgar, Moks & Saag 2010; Hua *et al.* 2014).

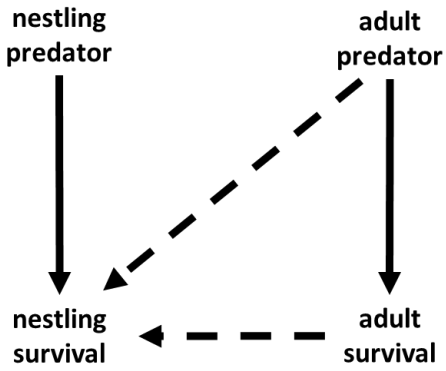

Figure 2-2. Differential effect of the presence of predators of nestlings and predators of adults. Nest predators only threaten offspring survival, predators of adults threaten directly adult survival and indirectly offspring survival. Solid lines: direct effects due to an attack from the predator. Dashed lines: indirect effects due to a modification of the parental behaviour from the presence of the predator or the death of a parent.

Previous comparative studies have shown that life-history pace (Ghalambor & Martin 2000; Ghalambor & Martin 2001) and the probability of re-nesting within a breeding season (LaManna & Martin 2016) influence parental investment responses to a perceived increase in

predation risk. In species with a slow life history pace, parents are more sensitive to predators that threaten their survival, while in species with a fast life history pace, parents are more sensitive to nest predators (Ghalambor & Martin 2000; Ghalambor & Martin 2001). In response to a high natural and experimental risk of nest predation, egg mass decreased for multiple-brooded species and increased for single-brooded species (LaManna & Martin 2016). Although these studies assessed specific drivers of parental decisions under predation risk, no previous study has investigated the relative importance of multiple drivers.

We hypothesise that life history, social system, and ecology may influence the costs and benefits associated with responses to risks of predation, and thus explain the plasticity in parental care strategies among species (Table 2-1). In accordance with life-history theory (Roff 1992; Stearns 1992) and previous field studies (Ghalambor & Martin 2000; Ghalambor & Martin 2001), we expect that species with a fast life-history pace (i.e., high current reproductive investment, low probability of future breeding) should have high costs from reduced offspring survival and thus, be particularly sensitive to nest predators. In contrast, species with a slow life-history pace (i.e., low current reproductive investment, high probability of future breeding) should have high costs from reduced adult survival and thus, be particularly sensitive to predators of adults ("life-history hypothesis"; Table 2-1). Independent of life-history pace, sociality can increase plasticity in parental care decisions by buffering out costs of predation risk ("social system hypothesis"; Table 2-1). In cooperatively breeding species, helpers may compensate for a decrease in parental care (Canestrari, Marcos & Baglione 2011) and thus, nestling condition is less likely to be compromised by the death of a parent or a temporary decrease in provisioning. In family-living species (Drobniak *et al.* 2015), a temporary decrease in provisioning could be compensated through extended post-fledging parental care. Finally, species with a higher brood value (i.e., low re-nesting probability and/or low nest failure) (Pianka & Parker 1975) should suffer most from reduced offspring survival, and thus be most sensitive to threats to their offspring ("brood value hypothesis"; Table 2-1).

Table 2-1. The three non-mutually exclusive hypotheses considered in this study and the variables used in the analyses.

hypotheses (related predictors included in the statistical analyses)	**attributes**	**associated conditions**	**consequences on costs-benefits balance → expected responses**
"life-history hypothesis" (brood size, body mass, maximum longevity)	fast life-history pace (i.e., large brood size, small body size, short-lived)	high investment into current reproduction low probabilities for future reproduction	breeding parents should benefit more from an increase in survival of their offspring, and thus, be less willing to engage in nest visitation patterns that will put their offspring at risk [(1-3)]
	slow life-history pace (i.e., small brood size, large body size, long-lived)	low investment into current reproduction high probabilities for future reproduction	breeding parents should benefit more from surviving to the next breeding season, and thus, be less willing to engage in nest visitation patterns that will enhance own predation risk [(1-3)]
"brood value hypothesis" (re-nesting potential within the breeding season, nest predation rate, nesting modus)	low re-nesting potential within the breeding season	high brood value (value of a current brood increases with the cost of replacing it [(4, 5)])	breeding parents should benefit more from an increase in survival of their current offspring, and thus, should engage more in behaviour that will enhance nest survival [(6-8)]
	low nest failure during the breeding season (i.e., good environmental conditions, low ambient predation, low nest accessibility (e.g. cavity-nester))	high brood value (nests with low probabilities to fail might be more valuable for parents than nests with low chance to succeed)	breeding parents should benefit more from an increase in survival of their current offspring, and thus, should engage more in behaviour that will enhance nest survival [(9)]
"social system hypothesis" (post-fledging parent-offspring association time)	group-living	protection from other group members (e.g. increasing vigilance or predator mobbing (distracting its attention away from the nest area or other group member) [(10-13)]	breeding parents should suffer less costs , and thus, should care less from being seen around the nest in the presence of an adult's or a nest predator
	cooperative breeding	the risk of decreased offspring condition from the death of an adult might be less detrimental as the nestling will be fed by the remaining adult and allofeeder(s)	breeding parents should suffer less costs, and thus, should care less from being seen around the nest in the presence of a predator of adults
	long post-fledging parent-offspring association time (e.g. family-living [14])	potential for compensation for the detrimental effect on their offspring after they live the nest	breeding parents should suffer less costs, and thus, should care less about the direct repercussion on their offspring condition from their behavioural decision

[1] (Williams 1966), [2] (Montgomerie & Weatherhead 1988), [3] (Roff 1992), [4] (Dawkins & Carlisle 1976), [5] (Boucher 1977), [6] (Clark 1994), [7] (Clutton-Brock 1991), [8] (Montgomerie & Weatherhead 1988), [9] (Ghalambor, Peluc & Martin 2013), [10] (Scheuerlein & Gwinner 2006), [11] (Ricklefs 1980), [12] (Boland 1998), [13] (Krause & Ruxton 2002b), [14] (Drobniak *et al.* 2015)

Here we test the relative importance of these hypotheses (Table 2-1) by consecutively exposing nests of 12 altricial bird species to an increased perceived risk of adult or nestling predation and assessing changes in nest visitation rates. To investigate parental trade-off between survival and reproduction, (i) we compared the species response to each predator type, and (ii) we assessed the variation among species in responses specific to a predator of adults.

2.2 Materials and Methods

2.2.1 SPECIES STUDIED AND STUDY SITES

We investigated parental care decisions in 12 altricial bird species that vary in their life history, ecology and social system (Table 2-S1, Supporting information; Figure 2-S1). These species comprise two taxonomic orders and nine families, including Iberian azure-winged magpie (*Cyanopica cooki*), black wheatear (*Oenanthe leucura*), common blackbird (*Turdus merula*), Eurasian blue tit (*Cyanistes caeruleus*), Eurasian magpie (*Pica pica*), European bee-eater (*Merops apiaster*), great tit (*Parus major*), hoopoe (*Upupa epops*), long-tailed tit (*Aegithalos caudatus*), red-billed chough (*Pyrrhocorax pyrrhocorax*), spotless starling (*Sturnus unicolor*) and woodchat shrike (*Lanius senator*). The study was conducted in four locations in Andalusia, Southern Spain (Table 2-S2 for details on the study sites). All species were studied in natural nests, except for Eurasian blue tit, great tit and spotless starling that were studied in nest boxes.

2.2.2 GENERAL FIELD AND EXPERIMENTAL PROCEDURE

Data were collected during the breeding seasons years 2010-2014 (from April to July; Table 2-S1). Nests were located during the building phase and monitored regularly to determine the start of egg-laying and the hatching date. We manipulated the perceived risk of predation using vocalizations and the presentation of taxidermic models of common predators of adults or nestlings of each species (mean = 12 nests per species, range = 8-15 nests per species; Table 2-

S3). We assessed their effect on nest visitation rates, which closely corresponds to the nestling provisioning rate (Schwagmeyer & Mock 2008; Mariette *et al.* 2011; Mutzel *et al.* 2013). In comparative studies, it is preferable to use the same experimental stimulus for each species. However, the same stimulus may not have a comparable effect (i.e., different species have different principal predators of adults and nestlings), and thus, we used different models that functionally are comparable (i.e., using common predators of adults and nestlings).

We determined the nest visitation rate with cameras mounted inside the nest boxes or near the natural nests, at a distance that did not disturb the focal individuals (i.e., that did not make parents hesitate to visit the nest). We mounted models on a 1.5-2m high pole, 10-15m away from the nest, and placed a camouflaged playback system (speaker, mp3 player, battery) below the models to playback the vocalization of the respective species. We used 15-30 different calls of 25-35sec length, played in random order, followed by 215-205sec of silence, resulting in one call each 4min. The calls were obtained from Xeno Canto (http://www.xeno-canto.org) and assembled in the software Audacity (http://www.audacityteam.org/). We performed the experiments when nestlings were within 1-2 days of their pin feathers breaking their sheath to control for the effect of nestling age on nest visitation rate.

In most cases, we used a model together with a playback to ensure the detection of the predator by the focal individuals. However, the experimental stimuli differed across and within species (Table 2-S4) for biological and logistic reasons. We presented only vocalizations to simulate the presence of corvids (i.e., common nest predators of open nesting species) and goshawk *Accipiter gentilis* (i.e., common predator of adults in large-sized birds: Kenward 2010). Exposure to a corvid or goshawk model generated intense group mobbing, involving focal individuals and other species (see also Ghalambor & Martin 2001). Such group mobbing could deviate the behaviour of the focal parents toward behaviours independent of predator defence (e.g. territorial behaviour), and thus confound their behavioural responses to our experiment.

Exposure to vocalizations only still generated behavioural responses. Common nest predators of cavity breeding species (woodpeckers, small mammals) and the common predator of adults of small and medium-sized species (sparrowhawk *Accipiter nisus*) (Newton 1986) did not generate such group mobbing, thus we used both models and vocalizations. We used only a model for the ocellated lizard *Timon lepidus*, a common nest predator of Eurasian bee-eater, since they do not produce vocalizations. Three nestling predator treatments in black wheatears did not involve a model due to field logistics. We note that excluding these experiments does not change the results qualitatively (Table 2-S5 and 2-S6). We exposed experimental nests to non-predatory species and always matched the presentation modus (calls and/or model) to that of the predator treatments to control for the experimental set-up. When the presentation modus differed between the two predator treatments, we used the one involving the most stimuli for the control treatment (Table 2-S4).

2.2.3 EXPERIMENTAL DESIGN

All experimental nests were consecutively exposed to three treatments (control, predator of adults, nestling predator) over one day in counter-balanced order within species (i.e., randomly choosing among the six possible treatment orders without replacement, repeating this process if required). Each treatment included a 90min pre-exposure session and a 90min exposure session, where we presented the corresponding model and/or vocalisations (Table 2-S4). The pole and the playback equipment were present also during the pre-exposure to control for their presence. Having a pre-exposure session for each treatment provided a control for variation in visitation rates at different times of the day. Each nest received a 60min break after each exposure session and before the next treatment (model and/or pole taken away (when appropriate), playback and camera stopped). In 32 out of 144 cases, we were unable to finish the whole experimental block on the same day due to adverse weather conditions or technical issues. Missing treatments were carried out 24 hours later.

2.2.4 STATISTICAL ANALYSES

In four species, parents changed the nest visitation rate between the pre-exposure and the exposure session in the control treatment, suggesting that they responded to the experimental set-up (Figure 2-S2). In order to control for its effect, we scaled the change in visitation rate observed in the predator treatments by the change in visitation rate observed in the control treatment:

$$\textit{Scaled change in visitation rate}_P = \frac{\frac{visitation\ rate\ exposure\ session_P}{visitation\ rate\ preexposure\ session_p}}{\frac{visitation\ rate\ exposure\ session_C}{visitation\ rate\ preexposure\ session_C}}$$

where P refers to the adult or the nestling predator treatment and C to the control treatment. In some cases, we observed no visits to the nest during a session, and thus we added 1 to all values to allow for division. The value of the formula's numerator informs whether parent's visitation rate increased (ratio superior to one) or decreased (ratio inferior to one) due to an exposure to the respective predators, relative to the baseline visitation rate (i.e. pre-exposure). To conserve the latter important information, we attributed a sign to the scaled change in visitation rate: a positive sign for an increase and a negative sign for a decrease. We log-transformed the scaled change in visitation rate prior to attributing it the sign to solve an issue of binomial distribution of models' residuals and to approximate a normal distribution. This log transformed and signed scaled change in visitation rate was used as the response variable in our models and we refer to it hereafter as "response in visitation rate". Note that a response in visitation rate of zero indicates no difference in the response to the respective predator treatment compared to the control treatment.

A more common approach to control for the effect of the experimental set up would have been to use the ratio pre-exposure/exposure session as the response variable, adults' vs nestlings' predator as the treatment factor and the ratio of pre-exposure/exposure session of the control

treatment (C_{ratio}) as a covariate in our models. However, this would have required the inclusion of several 3-way interactions to assess our hypotheses (e.g., treatment x life-history x $C_{ratio,}$ treatment x social system x C_{ratio}…). The statistical power of our analysis did not allow it. By calculating the *scaled change in visitation rate* we solved both issues, the 3-way interactions and any effects of the experimental set-up.

We included the following explanatory variables in the statistical analyses to test our three non-exclusive hypotheses (Table 2-1; detailed descriptions of all parameters are given in Table 2-S7): brood size, maximum longevity, log-transformed body mass, re-nesting potential (probability of additional breeding attempt(s) within the current breeding season), nest type (cavity or open nesting), nest predation rate, and log transformed post-fledging parent-offspring association time. Apart from brood size, which was nest-specific to also control for the fact that a higher number of nestling might imply higher nest visitations, all factors were species-specific (Table 2-S7). We also included the log transformed daily precipitation, the daily temperature, the date of the experiment and the time of the start of the predator treatment to control for the environmental and experimental design effect between nests or years (Table 2-S7). Species with high natural nest visitation rates might have higher plasticity in the visitation rate. However, including the natural nest visitation rates in the full model generated multicollinearity with maximum longevity, post-fledging parent-offspring association time and body mass. Since smaller bird species had higher natural nest visitation rates than larger species (correlation species average visitation rate – log (body mass): slope = -0.08, $r_{Spearman}$ = -0.77, $p < 0.005$), body mass partly controlled for natural potentials for plasticity in visitation rate. All continuous variables were centred (around the mean) and scaled (by the standard deviation) for the statistical analyses (Schielzeth 2010), but we present raw data in the figures. We checked the variance inflation factor (VIF) on the set of variables included in the full models (Dormann *et al.* 2013) using the function *vif.mer* (https://github.com/aufrank/R-hacks/blob/master/mer-utils.R). The VIF in all models were less than 2.9, which indicates an acceptable amount of covariance among predictors.

Statistical analyses were carried out in R version 3.0.2 (R Core Team 2013 version 3.0.2; http://www.R-project.org/). We fitted linear mixed-effects models (lmer function, lme4 package: Bates *et al.* 2014). We used a model selection and model averaging approach (Grueber *et al.* 2011) to determine the most important explanatory variables of the variation in the change in visitation rate (MuMIn package: Barton 2013). The candidate model set included models with ΔAICc ≤ 3 (Burnham & Anderson 2011), ΔAICc being the AICc of the focal model minus the AICc of the best model. The relative importance of a predictor was calculated by summing the Akaike's weights of the models in the candidate model set including the focal predictor, following the method described by Symonds and Moussalli (2011). The non-independence due to common evolutionary history among the 12 species was previously tested on both the null and full models using ASReml phylogenetic controlled mixed models (ASREML-R package: Butler 2009; VSN International, Hempstead, U.K.) (for more details see Table 2-S8). The phylogenetic effect was always non-significant (Table 2-S8), and accordingly, there was no need to control for phylogeny in our models.

To investigate differences in parental decision-making to risk among species, we first applied a model selection and averaging approach on a full model including predator type (predators of adults vs. nestlings) and its interaction with all above-mentioned parameters. The unit of analysis was the response in visitation rate to the adult and nestling predator treatment at each nest of each species. Species, year and nest identity were included as random factors to control for the non-independence of data. The z-test p-value of the averaged predator type parameter indicates if the response of the parents significantly differs between the two predator treatments (predator of adults, nestling predator). Second, to determinate if the change in nest visitation rate for each predator treatment significantly differed from that of the control treatment, we examined the 95% confidence interval (95% CI) of the unstandardized averaged least square means of each predator type (using lsmeans function (lsmeans package: Russell 2016)) and verified that they did not include the value of zero (i.e., response to the predator treatments equal to the response to the control treatment, see above).

The behavioural decision of parents to avoid risks to themselves may also compromise the condition of the nestlings if it implies a reduction of nest visitation. Consequently, exposure to a predator of adults *per se* may be responsible for a parental trade-off in decision-making (see introduction). Hence, we also investigated the change in nest visitation rates specific to the predator of adults. The unit of analysis was the response in visitation rate to the adult predator treatment at each nest of each species. Species and year were included as random factors. The full model included the same simple effects as in the previous analysis and additionally included the relative predation risk of adults (assessed as the prey's body mass over predator's body mass; Table 2-S7), but excluded predator type. We expected species with a high adult relative predation risk to respond more strongly to an adult predator. To investigate if the effect of proximate predation pressure on visitation rate was dependent on ultimate effects of predation pressure, the interaction between the nest predation rate and nest type was included.

2.3 Results

The main predictors of the variation in the response in visitation rate among species were predator type, re-nesting potential, maximum longevity and nest type (relative importance ≥ 0.95) (Table 2-2). Compared to the control treatment, species reduced their nest visitation rate only when adults were at risk (estimate: -0.16 (-0.31, 0.00); mean and 95% CI, also hereafter), but not when exposed to a predator of nestlings (estimate: 0.10 (-0.05, 0.26)) (Table 2-2 and Figure 2-3). The interaction between predator type and life-history, ecological, or social parameters had very low relative importance (< 0.20) or were absent from the candidate model set (Table 2-2 and 2-S9). In addition, a decrease in the nest visitation rate was associated with lower re-nesting potential within the current breeding season (estimate: 0.18 (0.03, 0.34)), a shorter lifespan (estimate: 0.28 (0.09, 0.48)), or open nests (open-nesting species estimate: -0.21 (-0.40, -0.02); closed-nesting species estimate: 0.15 (-0.01, 0.31)) (Figure 2-4a-c). Phylogeny did not influence the response in nest visitation rate (likelihood ratio test: LRT < 0.001, df = 1, p = 1, Table 2-S8).

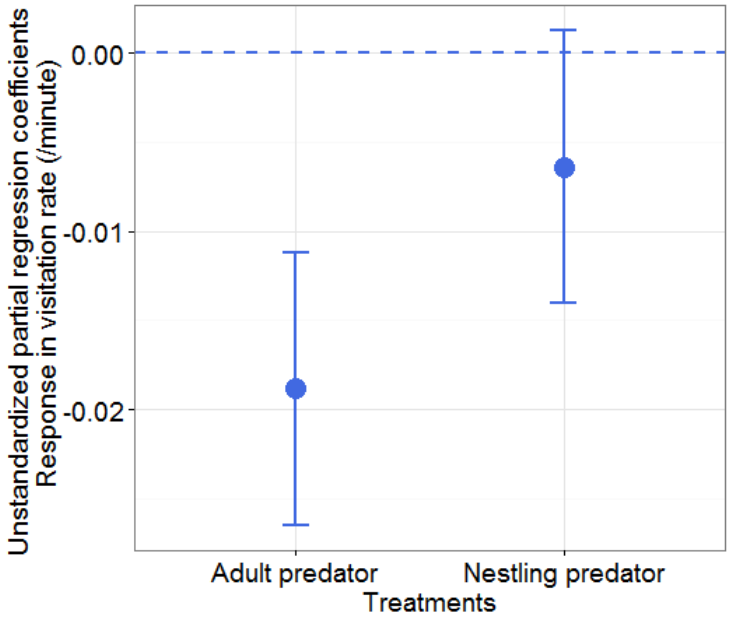

Figure 2-3. Difference in parental visitation rate (per minute) between adult and nestling predator treatment (unstandardized partial regression coefficients and 95% CI). The dashed line represents equality of response between control and predators treatments. If the 95%CI overlaps this dashed line (includes the value of zero), it means that the responses to the predator and the control treatments do not differ significantly. The further away from this line the higher the response. Positive values indicate an increase in response and negative values a decrease. For graphical details on the differences between the pre-exposure and exposure sessions of each treatment within species see Figure 2-S2 and among species see Figure 2-S3.

Assessing the response specific to an increased risk of adult predation showed that the decrease in nest visitation rate was higher in species with a low re-nesting potential than in species with a high re-nesting potential (relative importance: 0.84: Table 2-3 and Figure 2-5). All other parameters had lower relative importance (<0.75), or were absent from the candidate model set (Table 2-3 and 2-S10). The phylogenetic effect was not significant (likelihood ratio test: LRT = 0.002, df = 1, p = 0.97, Table 2-S8).

Table 2-2: Standerdized predictors coefficients and their relative explanatory importance for the analysis of adults' vs. nestling's predation risk.

Predictors		Predictors ' relative importance	Model Averaging estimates*,†	95% CI
simple effects				
Intercept			0.02	(-0.19, 0.24)
predator type	adult	1.00	na	na
	nestling		0.26	**(0.05, 0.47)**
nest brood size		0.05	-0.00	(-0.14, 0.14)
ln(adult body mass)		0.56	-0.07	(-0.27, 0.03)
maximum longevity		1.00	0.28	**(0.09, 0.48)**
nest type	closed	0.95	na	na
	open		-0.37	**(-0.70, -0.07)**
nest predation rate		0.05	0.00	(-0.13, 0.14)
re-nesting potential		0.95	0.18	**(0.03, 0.34)**
ln(post-fledging parent-offspring association time)		0.83	0.13	(-0.00, 0.32)
ln(daily precipitation)		0.05	-0.00	(-0.13, 0.11)
daily temperature		0.06	-0.00	(-0.16, 0.09)
date of the experiment		0.09	-0.00	(-0.18, 0.08)
time of the start of the treatment		0.09	-0.00	(-0.15, 0.07)
Interactions				
predator type: ln(adult body mass)	adult	0.06	na	na
	nestling		-0.00	(-0.28, 0.14)
predator type: maximum longevity	adult	0.05	na	na
	nestling		0.00	(-0.18, 0.24)
predator type: nest type	closed: adult	0.05	na	na
	closed: nestling		na	na
	open: adult		na	na
	open: nestling		-0.00	(-0.48, 0.36)
predator type: re-nesting potential	adult	0.17	na	na
	nestling		-0.02	(-0.32, 0.10)
predator type: ln(post-fledging parent-offspring association time)	adult	0.05	na	na
	nestling		-0.00	(-0.22, 0.20)

*: model averaging estimates according to full model averaging approach since the best AICc model is not strongly weighted (weight = 0.09)(Symonds & Moussalli 2011); they are based on 32 models with Δ AICc ($AICc_{focal\ model} - AICc_{best\ model}$) ≤ 3, see Table 2-S9; §: reference levels of categorical variables have an estimate of 0; na – not applicable; 95% CI – 95% confidence interval, in bold are presented the 95% confidence intervals that do not overlap zero.

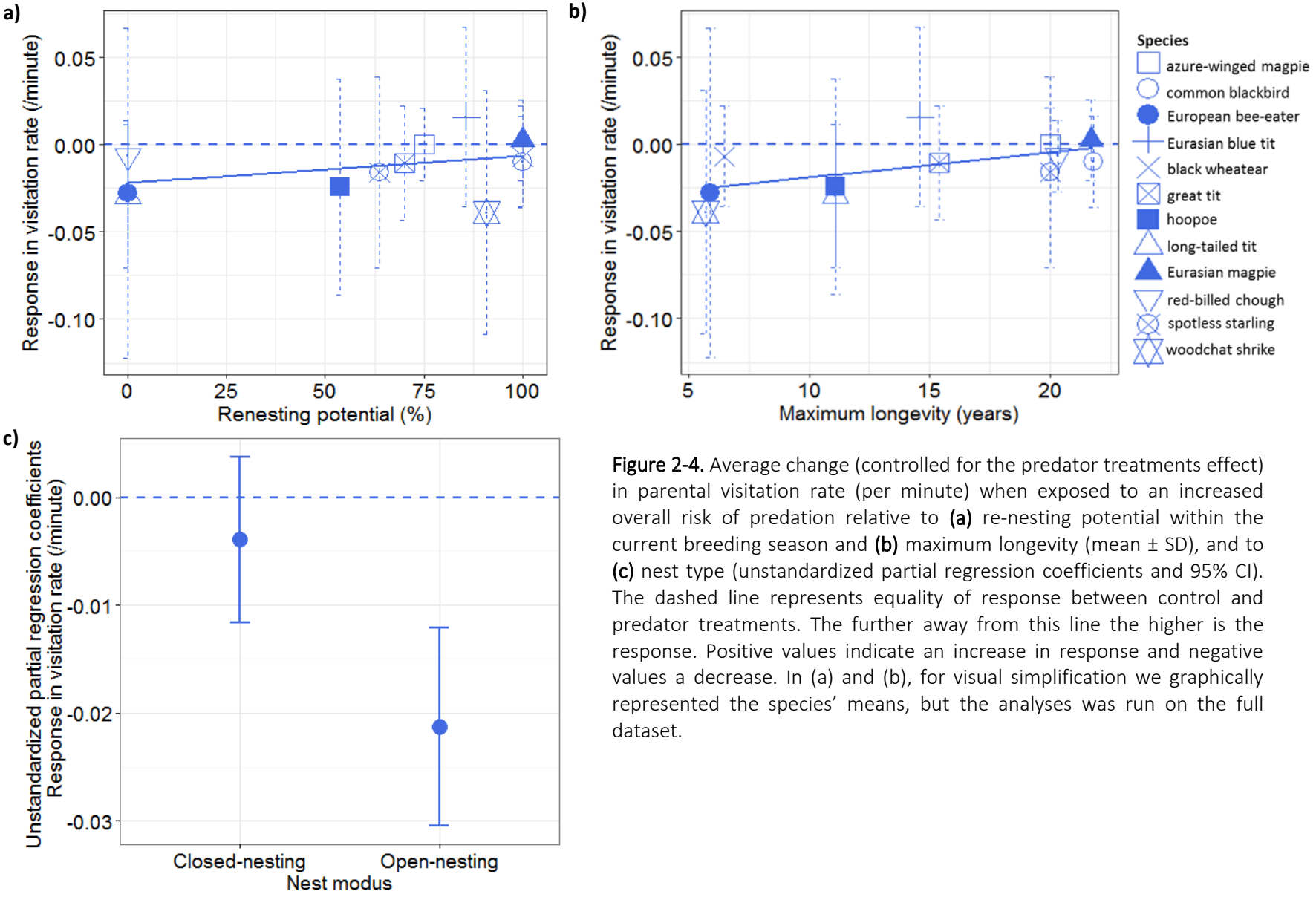

Figure 2-4. Average change (controlled for the predator treatments effect) in parental visitation rate (per minute) when exposed to an increased overall risk of predation relative to **(a)** re-nesting potential within the current breeding season and **(b)** maximum longevity (mean ± SD), and to **(c)** nest type (unstandardized partial regression coefficients and 95% CI). The dashed line represents equality of response between control and predator treatments. The further away from this line the higher is the response. Positive values indicate an increase in response and negative values a decrease. In (a) and (b), for visual simplification we graphically represented the species' means, but the analyses was run on the full dataset.

2.4 Discussion

Parental responses to predation risk during nestling provisioning may be short-term, with potential long-term fitness consequences (Lima 2009; Zanette *et al.* 2011). Responses to a nest predator are likely to influence current reproduction, and show whether parents value nest failure over the health of the current brood. A predator of adults, however, may affect both current reproduction, through a reduction of parental care, and future reproduction through predation of a parent. Responses to a predator of adults may therefore reflect sensitivity to indirect risks to nestlings and direct risks to parents. Our comparative study shows that birds adjust their parental care strategies depending on the type of predation risk, where species responded only to a predator of adults. In addition, under a generally increased predation risk, species with a low probability of re-nesting within the breeding season, a short lifespan, or with open-nests, particularly reduced their nest visitation rate.

Decreased nest visitation rates in the presence of a predator of adults could reflect that parents invest their time into other behaviours beneficial for offspring condition and survival, such as predator mobbing (Mutzel *et al.* 2013; Schneider & Griesser 2015) or nest-attending behaviours (Wiebe & Elchuk 2003). Yet, we found no change in the average time parents spent in the nest under increased perceived risk of predation (Figure 2-S4) and the change in visitation rate and mean duration of visits did not depend on each other (adult predator treatment: slope = -1.04, $r_{Spearman}$ = -0.05, p = 0.58; nestling predator treatment: slope = -1.04, $r_{Spearman}$ = -0.05, p = 0.58 (details per species in Figure 2-S5); both treatments combined: slope = -0.72, $r_{Spearman}$ = -0.07, p = 0.23). Thus, while parents may have invested time in predator mobbing, it is unlikely that they redirected parental care to nest-attentiveness.

Table 2-3: Standerdized predictors coefficients and their relative explanatory importance for the analysis of adults' predation risk.

predictors		Relative importance of predictors	Model averaging estimates*,†	95% CI
intercept			0.05	(-0.20, 0.31)
nest brood size		0.18	-0.02	(-0.30, 0.10)
ln(adult body mass)		0.09	0.00	(-0.18, 0.28)
maximum longevity		0.75	0.16	(-0.03, 0.44)
nest type	closed	0.36	na	na
	open		-0.11	(-0.73, 0.12)
nest predation rate		0.28	-0.03	(-0.28, 0.07)
re-nesting potential		0.84	0.15	**(0.00, 0.36)**
ln(post-fledging parent-offspring association time)		0.24	0.04	(-0.08, 0.40)
adult relative predation risk		0.50	-0.08	(-0.35, 0.04)
ln(daily precipitation)		0.11	-0.01	(-0.24, 0.10)
daily temperature		0.07	0.00	(-0.17, 0.17)
date of the experiment		0.08	-0.00	(-0.24, 0.16)
time of the start of the treatment		0.07	0.00	(-0.16, 0.16)

*: model averaging estimates according to full model averaging approach since the best AICc model is not strongly weighted (weight = 0.03) (Symonds & Moussalli 2011), They are based on 102 models with Δ AICc ($AICc_{focal\ model} - AICc_{best\ model}$) ≤ 3, see Table 2-S10; §: reference levels of categorical variables have an estimate of 0; na – not applicable; 95% CI – 95% confidence interval, in bold are presented the 95% confidence intervals that do not overlap zero

Across species, predator type influenced nest visitation rates (Figure 2-3 and Table 2-2), supporting the idea that birds adjust their behaviour to the risks of predation in ecological time (Lima 2009; Hua *et al.* 2014). Previous studies found a change in parental behaviour under increased risk to offspring (Fontaine *et al.* 2007; Martin & Briskie 2009; Ibanez-Alamo & Soler 2010), or under both an increased risk to offspring and adults (Ghalambor & Martin 2000; Ghalambor & Martin 2001). In contrast, we found a reduction in nest visitation rate only when parents were exposed to an increased predation risk to adults but not in response to an increased risk to offspring (Figure 2-3 and Table 2-2). A study on the short-lived, cavity-nesting pied flycatcher (*Ficedula hypoleuca*) obtained comparable results. Parents only reduced their provisioning rate when exposed to a predator of adults but no behavioural change was found when nest predation was simulated (Tilgar, Moks & Saag 2010). The observed responses may arise as the chances of current brood survival and future reproduction will be reduced or null if parents are injured or die. These fitness costs to the parents may be higher than from a decrease in current offspring condition or survival, as implied by the absence of response to a nestling predator. Overall, breeding parents seemed to favour their own survival over offspring condition.

Interestingly, the effect of the predator type on the change in nest visitation rate was independent of the life history, ecology or social system of the species (Table 2-2). Nevertheless, re-nesting potential, longevity, and nest type are important predictors of the variation in responses among species when overall predation risk, or adult predation risk only (specifically re-nesting potential) were considered (Tables 2-2 and 2-3 and below).

2.4.1 EFFECT OF RE-NESTING POTENTIAL

Our results highlight that re-nesting potential influences parental care strategies in response to risk among species. This result supports a finding from a previous comparative field experiment which demonstrated the role of re-nesting potential (single- vs. multiple-broods) in shaping parental responses during the incubation period under increased risk of nest predation (LaManna & Martin

2016). Our results showed that species with a lower probability to breed again within the breeding season responded more strongly than species with higher re-nesting potential by markedly reducing their nest visitation when exposed to an increased predation risk in general (Figure 2-4a) and to a predator of adults only (Figure 2-5). To our knowledge, our study demonstrates for the first time the role of re-nesting potential in shaping parental responses during the nesting period when parents are at risk.

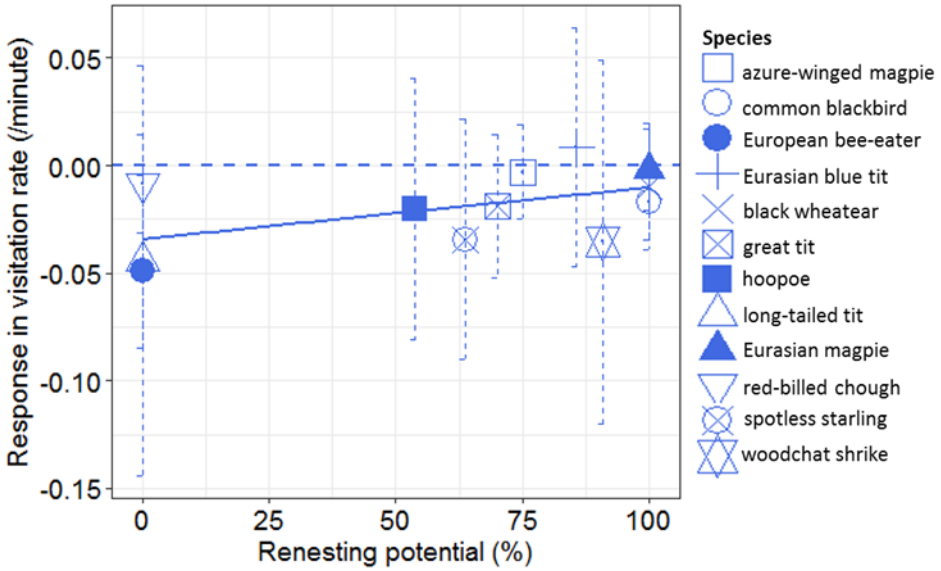

Figure 2-5. Change in parental visitation rate (per minute) when exposed to a predator of adults relative to the re-nesting potential (mean ± SD). The dashed line represents equality of response between control and predators treatments. The further away from this line the higher is the response. Positive values indicate an increase in response and negative values a decrease. For visual simplification, we graphically represented the species' means, but the analyses were run on the full dataset.

Given that the value of a brood increases with the cost of replacing it (Dawkins & Carlisle 1976; Boucher 1977), species with high probability of re-nesting should have lower brood value than species that are unlikely to replace a failed nest. Hence, our results support that the value of a brood can be an important driver of parental care strategies (Montgomerie & Weatherhead 1988; Dale, Gustavsen & Slagsvold 1996; LaManna & Martin 2016). More specifically, they suggest that species with high brood value seem to be more sensitive to risks of predation than species with low brood value. If nest visitation is exchanged for increased mobbing behaviour (Mutzel *et al.* 2013; Schneider & Griesser

2015), the stronger response of species with higher brood value could be a strategy to make the predator leave the nest location sooner, thereby limiting subsequent costs to valuable offspring.

2.4.2 EFFECT OF LONGEVITY

Life-history theory predicts that species with a slow life-history pace should be more sensitive to risks to themselves than to their offspring, and the opposite is expected for species with fast life-history pace (Williams 1966; Montgomerie & Weatherhead 1988; Roff 1992) (Table 2-1). Accordingly, a previous comparative study found that differences in the reduction of parental provisioning in response to a predator of adults or nestlings depended on the species life-history pace (Ghalambor & Martin 2001). We found no interaction between predator type and longevity, but found that short-lived species generally responded more strongly to predation risks than long-lived species (Table 2-2 and Figure 2-4b). The difference in the results between the studies may reflect that we compared species from a limited geographic range experiencing similar ecological conditions, while the previous study compared species from the northern and southern hemisphere.

Our result suggests that short-lived species are more sensitive to predation risk than long-lived species. Individuals of long-lived species are more likely to be experienced and have reproduced successfully prior to our experiment, compared to individuals in short-lived species, which may influence how species respond to an increased predation risk. A test of the effect of an individual's age on parental responses to risk could assess this hypothesis, but we lacked information on the age of the majority of our experimental individuals. Furthermore, long-lived species are usually larger (de Magalhaes, Costa & Church 2007; Wasser & Sherman 2010), reducing predation pressure (Valcu *et al.* 2014) and allowing them to better defend themselves against predators (Lima 1986), lowering their risk sensitivity. Longevity and body mass correlated positively in our set of species (Figure 2-S6). Nevertheless, body mass appears in only about 50% of the set of "best models" and its presence did not seem to alter the mean estimates of longevity (Table 2-S9). While correlated with longevity, body

size may not be a major predictor of the variation in responses among our set of species (see also Figure 2-S7).

2.4.3 EFFECT OF NEST TYPE

Only open-nesting species reduced their visitation rate under increased risks of predation (Figure 2-4c), which may reflect variation in natural vulnerability depending on nest type (Fontaine *et al.* 2007). This result is in accordance with previous studies suggesting that individuals or species with higher nest vulnerability cannot afford to adopt the same behaviours as those with lower nest vulnerability (Martin & Ghalambor 1999; Martin, Scott & Menge 2000; Fontaine *et al.* 2007). Furthermore, under increased predation risk, provisioning rates decreased more in species that had a greater ambient risk of predation (Ghalambor, Peluc & Martin 2013). However, in our study nest predation rate did not have notable explanatory power (Table 2-2 and 2-3). In addition, cavity nests might be easier to defend against predators, as the area for potential attacks is small. Moreover, cavities can offer a safe shelter to the parents if threatened by an aerial predator. Therefore, maintaining the number of nest visits when exposed to general predation risks could reflect a strategy for keeping offspring and parents secure in cavity-nesting species.

2.4.4 CAVEATS

Since we used the most important predator known as the experimental stimulus for each species, the perceived predation risk may have differed across species. The perceived predation risk is likely to depend on predator abundance (Lima 2009), habitat cover, body size or prey profitability (Götmark & Post 1996). For instance, the relative risk of being killed by a sparrowhawk decreases with increasing foraging height (Götmark & Post 1996). However, the different types of habitat (e.g., relatively open or closed; Table 2-S2), which are also likely to vary in their predator abundance, seem equally represented along the continuum of responses (Figures 2-4a and 2-4b). Body size was not a major predictor of the change in visitation rate (Table 2-2 and 2-3) and prey profitability (body

mass/predator body mass; Table 2-S7) explained little of the variation in the responses to a predator of adults (relative importance: 0.50, estimate: -0.08 (-0.35, 0.04); Table 2-3). Moreover, including species as a random factor should, at least partially, control for species-specific perceived predation risk. Hence, while we cannot exclude the influence of a differential perceived threat among species, it seems that it may only have a marginal effect on our results.

Further studies including more species, a larger sample size and a larger spectrum of life histories, ecologies and social systems would help elucidate the relative importance of the different hypotheses considered in this study. Additionally, responses to mammalian predators of adults or nestlings could elicit different behavioural responses (Bures & Pavel 2003). Hence, comparative experimental studies involving different categories of predators would help to generalize our findings.

2.4.5 CONCLUSION

To conclude, our comparative study shows that increased predation risk induces a change in parental nest visitation rates, supporting that birds are able to adjust their responses to the type of predator in ecological time (Lima 2009). However, in contrast with previous studies (Eggers, Griesser & Ekman 2005; Martin & Briskie 2009; Zanette *et al.* 2011; Ghalambor, Peluc & Martin 2013; Grunst, Grunst & Rotenberry 2015), we did not find a decrease in nest visitation rate under increased nest predation risk. More importantly, our results suggest that species that are more vulnerable to predation, are more sensitive to an increased perceived risk of predation. Increased vulnerability may arise through higher chances of adult or nest predation (i.e. open nesters) or through high costs from the loss of the current brood, as is the case in species with low renesting potential and a short lifespan. Overall, our results reveal that the degree of plasticity in parental decision to risks among species is mainly influenced by short- and long-term reproductive prospects, and by the natural vulnerability to risk.

While numerous studies explored the influence of increased predation risk on parental investment strategies (reviewed by: Lima 2009; Ibáñez-Álamo *et al.* 2015), little is known about the

reason for the variation in the plasticity among species. To our knowledge, this is only the second large-scale comparative study investigating interspecific plasticity in responses to both adults' and nestlings' predators (Ghalambor & Martin 2001), and the first to do so in a limited geographical location. By investigating a larger array of potential explanatory factors and the response specific to a predator of adults, our study offers novel insight into the understanding of interspecific variation in parental care strategies under different risks of predation.

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Appendix Chapter 2

Table 2-S1. Information on the species studied.

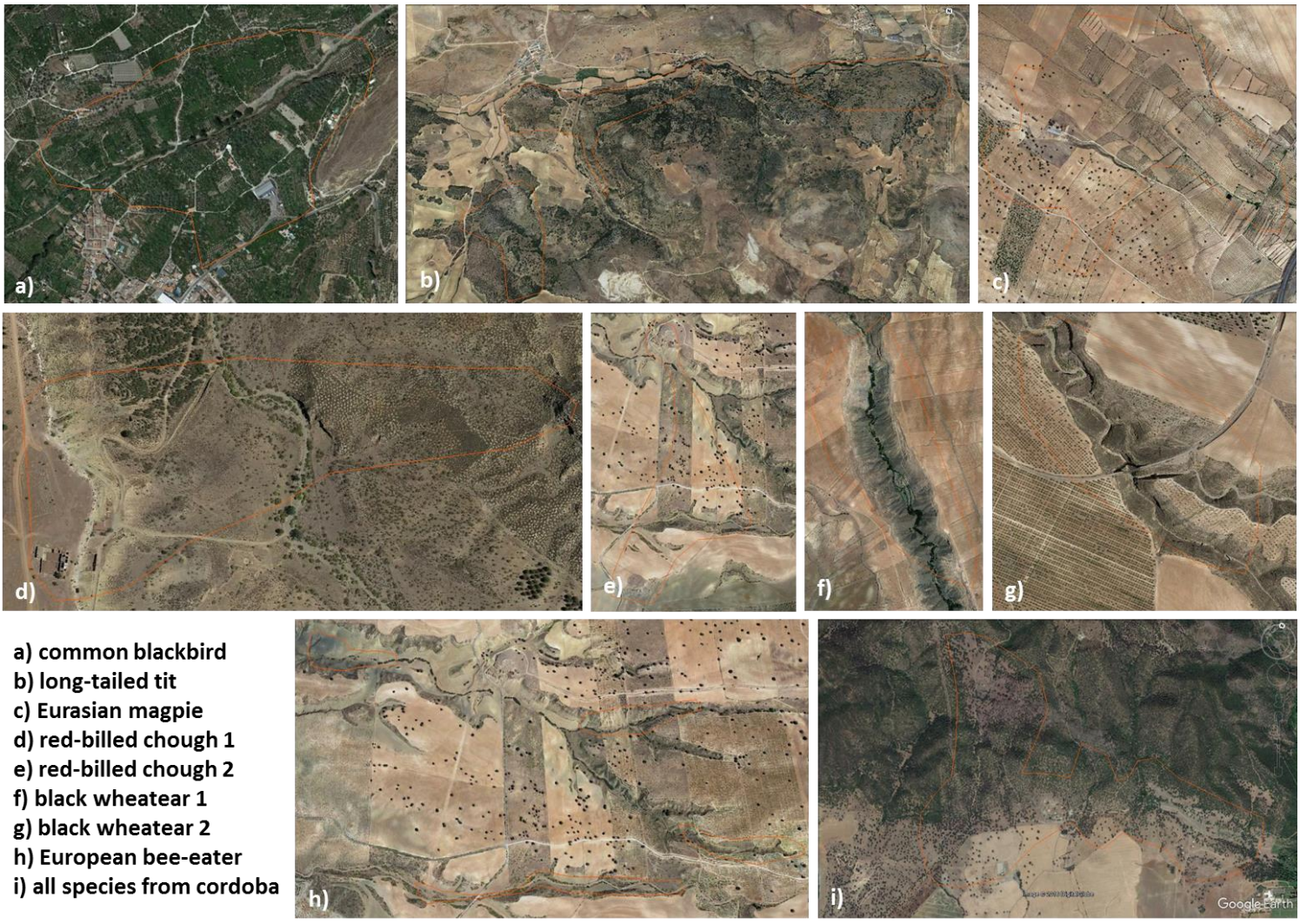
	visitation rate on normal conditions	social system		life-history						ecology			
species studied	**average visitation rate ± SD (per minute)**	**social system***	**post-fledging parent-offspring association time (days)**	**maximum longevity (years)**	**adult survival rate**	**body mass (grams)**	**average clutch size**	**average brood size**	**nestling period (days)**	**initiation breeding (in our populations)**	**nest type**	**average annual (2010 to 2014) nest predation (%)**	**average re-nesting probability**
azure-winged magpie	0.11 ± 0.05 (n=36)	CB	400.0	20.0	50.0	69.57 (n=213)	5.89 (n=93)	3.97 (n=33)	16.0	end March	open nester	20.4 (n=143)	75.0 (n=12)
black wheatear	0.13 ± 0.05 (n=45)	FL	180.0	6.5	49.5	36.45 (n=69)	4.02 (n=110)	3.42 (n=92)	15.0	start-mid April	closed nester	24.4 (N=149)	100.0 (n=15)
common blackbird	0.14 ± 0.06 (n=39)	PB	21.0	21.8	56.0	94.13 (n=31)	2.91 (n=99)	2.51 (n=78)	14.0	mid-March	open nester	23.3 (n=148)	100.0 (n=13)
Eurasian blue tit	0.43 ± 0.30 (n=42)	PB	17.5	14.6	41.6	9.36 (n=13)	7.34 (n=41)	6.52 (n=34)	18.5	mid-end March	closed nester	9.6 (n=61)	85.7 (n=14)
Eurasian magpie	0.06 ± 0.05 (n=42)	FL	75.0	21.7	69.0	178	6.46 (n=26)	4.05 (n=17)	27.2	end March-start April	open nester	36.3 (n=67)	100.0 (n=14)
European bee-eater	0.31 ± 0.20 (n=24)	CB	400.0	5.9	49.8	52.33 (n=71)	5.77 (n=75)	5.24 (n=55)	32.0	mid-end May	closed nester	22.3 (n=93)	0.0 (n=8)
great tit	0.19 ± 0.11 (n=30)	PB	31.5	15.4	48.6	17.47 (n=16)	7.53 (n=76)	5.98 (n=48)	18.0	start March	closed nester	19.6 (n=110)	70.0 (n=10)
hoopoe	0.28 ± 0.15 (n=39)	FL	75.0	11.1	41.1	67.1	6.23 (n=13)	3.1 (n=10)	27.5	mid-end April	closed nester	0 (n=23)	53.8 (n=13)
long-tailed tit	0.28 ± 0.09 (n=33)	CB	300.0	11.1	55.0	7.04 (n=35)	7.48 (n=52)	6.77 (n=22)	16.0	end March-start April	open nester	46.6 (n=87)	0.0 (n=11)
red-billed chough	0.05 ± 0.03 (n=36)	FL	42.0	20.3	80.0	277.8	4.42 (n=38)	4.14 (n=37)	36.0	mid-March	closed nester	16.4 (n=51)	0.0 (n=12)
spotless starling	0.18 ± 0.14 (n=33)	PB	7.0	20.0	49.9	82.32 (n=6)	4.60 (n=118)	4.01 (n=83)	21.0	start April	closed nester	20.1 (n=167)	63.6 (n=11)
woodchat shrike	0.36 ± 0.17 (n=33)	PB	42.0	5.7	54.0	28.51 (n=35)	5.07 (n=45)	4.12 (n=41)	15.0	end April-start May	open nester	35.1 (n=87)	90.9 (n=11)

n = sample size; SD = Standard deviation; CB = Cooperative breeding, PB = Pair breeding, FL = Family-living (Drobniak *et al.* 2015)

* all have biparental brood care (as opposed to uniparental). Data without sample size were not from our studied populations but were obtained from the literature (e.g. Del Hoyo *et al.* 2011; http://genomics.senescence.info/species/)

Table 2-S2. Details on each study site and aerial images. m.a.s.l: meters above sea level.

province	study site	species studied	coordinates	altitude (m.a.s.l.)	description
Granada	Valley of Lecrín	common blackbird	36° 56'N, 3° 33'W	580	dense orange groves
	Diezma	long-tailed tit	37° 20'N, 3° 20'W	1200-1400	sparse small holm oak tree forest
	Hoya de Guadix	black wheatear European bee-eater Eurasian magpie red-billed chough	37° 18'N, 3° 11'W	900-1100	deep canyons and ravines with eroded slopes, which cut into high plateau covered by sparse holm oak, almond tree field and agricultural crops
Cordoba	Alcolea	azure-winged magpie Eurasian blue tit great tit hoopoe spotless starling woodchat shrike	37° 56'N, 4° 42'W	160-330	hilly cow field covered by holm oak, olives trees and few crop field



a) common blackbird
b) long-tailed tit
c) Eurasian magpie
d) red-billed chough 1
e) red-billed chough 2
f) black wheatear 1
g) black wheatear 2
h) European bee-eater
i) all species from cordoba

*The distance between the farthest locations was 159km

Table 2-S3. Sample sizes of nests studied (each nest was exposed to each three treatment).

order	family	scientific name	common name	location studied	number of experiments
Coraciiformes	Meropidae	*Merops apiaster*	European bee-eater	Granada	8
Coraciiformes	Upupidae	*Upupa epops*	hoopoe	Cordoba	13
Passeriformes	Aegithalidae	*Aegithalos caudatus*	long-tailed tit	Granada	11
Passeriformes	Corvidae	*Cyanopica cooki*	azure-winged magpie	Cordoba	12
Passeriformes	Corvidae	*Pica pica*	Eurasian magpie	Granada	14
Passeriformes	Corvidae	*Pyrrhocorax pyrrhocorax*	red-billed chough	Granada	12
Passeriformes	Laniidae	*Lanius senator*	woodchat shrike	Cordoba	11
Passeriformes	Muscicapidae	*Oenanthe leucura*	black wheatear	Granada	15
Passeriformes	Paridae	*Cyanistes caeruleus*	Eurasian blue tit	Cordoba	14
Passeriformes	Paridae	*Parus major*	great tit	Cordoba	10
Passeriformes	Sturnidae	*Sturnus unicolor*	spotless starling	Cordoba	11
Passeriformes	Turdidae	*Turdus merula*	common blackbird	Granada	13
			total		**144**

Table 2-S4. Details on the type of stimulus used during the exposure session of each treatment for each species.

species studied	nestling's predator	model used	vocalization used	adult's predator	model used	vocalization used	control	model used	vocalization used
azure-winged magpie	*Corvus corax* (common raven)	NO	YES	*Accipiter nisus* (Eurasian sparrowhawk)	YES	YES	*Chloris chloris* (European greenfinch, N=7) or *Turdus merula* (common blackbird, N=5)	YES	YES
black wheatear	*Mustela nivalis* (least weasel, N=12) or	YES	YES	*Accipiter nisus* (Eurasian sparrowhawk)	YES	YES	*Chloris chloris* (European greenfinch, N=9) or *Alectoris rufa* (red-legged partridge, N=3) or *Columba palumbus* (common wood pigeon, N=3)	YES	YES
	Mustela nivalis (least weasel) & *Rattus norvegicus* (brown rat) (N=3)	NO	YES						
common blackbird	*Garrulus glandarius* (Eurasian jay) & *Pica pica* (Eurasian magpie)	NO	YES	*Accipiter nisus* (Eurasian sparrowhawk)	YES	YES	*Chloris chloris* (European greenfinch, N=9) or *Columba palumbus* (common wood pigeon , N=4)	YES	YES
Eurasian blue tit	*Picus viridis* (European green woodpecker, N=13) or *Dendrocopos major* (great spotted woodpecker, N=1)	YES	YES	*Accipiter nisus* (Eurasian sparrowhawk)	YES	YES	*Chloris chloris* (European greenfinch, N=1) or *Turdus merula* (common blackbird, N=8) or *Turdus philomelos* (song thrush, N=5)	YES	YES
Eurasian magpie	*Corvus corax* (common raven)	NO	YES	*Accipiter gentilis* (Northern Goshawk)	NO	YES	*Chloris chloris* (European greenfinch, N=5) or *Columba palumbus* (common wood pigeon, N=9)	NO	YES
European bee-eater	*Timon lepidus* (ocellated lizard)	YES	NO	*Accipiter nisus* (Eurasian sparrowhawk)	YES	YES	*Columba palumbus* (common wood pigeon)	YES	YES
great tit	*Picus viridis* (European green woodpecker)	YES	YES	*Accipiter nisus* (Eurasian sparrowhawk)	YES	YES	*Turdus merula* (common blackbird, N=5) or *Turdus philomelos* (song thrush, N=4)	YES	YES
hoopoe	*Picus viridis* (European green woodpecker, N=8) *Dendrocopos major* (great spotted woodpecker, N=5)	YES	YES	*Accipiter nisus* (Eurasian sparrowhawk)	YES	YES	*Turdus merula* (common blackbird, N=6) or *Turdus philomelos* (song thrush, N=7)	YES	YES
long-tailed tit	*Garrulus glandarius* (Eurasian jay) & *Pica pica* (Eurasian magpie)	NO	YES	*Accipiter nisus* (Eurasian sparrowhawk)	YES	YES	*Chloris chloris* (European greenfinch, N=2) or *Alectoris rufa* (red-legged partridge, N=2) or *Columba palumbus* (common wood pigeon, N=7)	YES	YES
red-billed chough	*Corvus corax* (common raven)	NO	YES	*Accipiter gentilis* (Northern Goshawk)	NO	YES	*Chloris chloris* (European greenfinch)	NO	YES
spotless starling	*Picus viridis* (European green woodpecker)	YES	YES	*Accipiter nisus* (Eurasian sparrowhawk)	YES	YES	*Turdus merula* (common blackbird)	YES	YES
woodchat shrike	*Garrulus glandarius* (Eurasian jay) & *Pica pica* (Eurasian magpie)	NO	YES	*Accipiter nisus* (Eurasian sparrowhawk)	YES	YES	*Turdus merula* (common blackbird, N=6) or *Turdus philomelos* (song thrush, N=5)	YES	YES

Table 2-S5: Standerdized predictors coefficients and their relative explanatory importance for the analysis of adults' vs. nestlings' predation risk excluding 3 black wheatears'nests.

predictors		Relative importance of predictors	Model averaging estimates*,†	95% CI
simple effects				
intercept			0.03	(-0.20, 0.25)
predator type	adult	1.00	na	na
	nestling		0.26	**(0.04, 0.47)**
nest brood size		0.05	-0.00	(-0.14, 0.15)
ln(adult body mass)		0.55	-0.07	(-0.27, 0.03)
maximum longevity		1.00	0.28	**(0.08, 0.47)**
nest type	closed	0.94	na	na
	open		-0.36	**(-0.71, -0.06)**
nest predation rate		0.05	0.00	(-0.13, 0.14)
re-nesting potential		0.94	0.17	**(0.03, 0.34)**
ln(post-fledging parent-offspring association time)		0.82	0.13	(-0.01, 0.32)
ln(daily precipitation)		0.05	-0.00	(-0.13, 0.12)
daily temperature		0.06	-0.00	(-0.16, 0.09)
date of the experiment		0.09	-0.00	(-0.18, 0.08)
time of the start of the treatment		0.09	-0.00	(-0.14, 0.08)
interactions				
predator type: ln(adult body mass)	adult	0.06	na	na
	nestling		-0.00	(-0.28, 0.14)
predator type: maximum longevity	adult	0.05	na	na
	nestling		0.00	(-0.18, 0.24)
predator type: nest type	closed: adult	0.05	na	na
	closed: nestling		na	na
	open: adult		na	na
	open: nestling		-0.00	(-0.48, 0.37)
predator type: re-nesting potential	adult	0.17	na	na
	nestling		-0.02	(-0.32, 0.10)
predator type: ln(post-fledging parent-offspring association time)	adult	0.05	na	na
	nestling		-0.00	(-0.22, 0.20)

*: model averaging estimates according to full model averaging approach since the best AICc model is not strongly weighted (weight = 0.09) (Symonds and Moussalli 2011), They are based on 32 models with Δ AICc (AICc focal model – AICc best model) ≤ 3, see Table 2-S6; §: reference levels of categorical variables have an estimate of 0; na – not applicable; 95% CI – 95% confidence interval, bold interval are not overlapping zero.

Table 2-S6. Adults' vs. nestlings' predation risk analysis excluding 3 black wheatears'nests - Model set obtained after model selection based on ΔAICc ≤ 3.

simple effects													interactions										model information				
(Intercept)	predator type	nest brood size	ln(adult body mass)	maximum longevity	nest type	nest predation rate	re-nesting potential	ln(association time)	ln(daily precipitation)	daily temperature	date of the experiment	time start	predator type: nest brood size	predator type: ln(adult body mass)	predator type: maximum longevity	predator type: nest type	predator type: nest predation rate	predator type: re-nesting potential	predator type: ln(association time)	predator type: ln(daily precipitation)	predator type: daily temperature	predator type: date of the experiment	predator type: time start	df	log Likelihood	AICc	Δ AICc	weight
0.05	+	-	-0.13	0.33	+	-	0.18	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-385.35	793.67	0.00	0.09
0.04	+	-	-	0.25	+	-	0.18	0.14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-386.79	794.39	0.72	0.06
0.05	+	-	-0.13	0.33	+	-	0.24	0.17	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	12	-384.78	794.73	1.06	0.05
-0.02	+	-	-	0.19	+	-	0.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-388.24	795.13	1.46	0.04
0.06	+	-	-0.12	0.34	+	-	0.19	0.17	-	-	-0.04	-	-	-	-	-	-	-	-	-	-	-	-	12	-385.12	795.39	1.72	0.04
0.04	+	-	-	0.25	+	-	0.23	0.14	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	11	-386.23	795.43	1.76	0.04
0.05	+	-	-0.09	0.33	+	-	0.18	0.17	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	12	-385.14	795.44	1.77	0.04
-0.13	+	-	-	0.18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-390.55	795.52	1.84	0.03
0.05	+	-	-0.13	0.33	+	-	0.18	0.17	-	-	-	-0.03	-	-	-	-	-	-	-	-	-	-	-	12	-385.20	795.55	1.88	0.03
-0.02	+	-	-0.09	0.24	+	-	0.12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-387.42	795.65	1.98	0.03
0.06	+	-	-0.12	0.32	+	-	0.19	0.17	-	-0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-385.26	795.68	2.01	0.03
0.05	+	-	-0.13	0.31	+	-	0.18	0.17	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	12	-385.30	795.77	2.09	0.03
0.04	+	-	-0.13	0.33	+	-	0.18	0.17	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	12	-385.31	795.78	2.11	0.03
0.05	+	-0.02	-0.13	0.33	+	-	0.18	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-385.32	795.81	2.13	0.03
0.05	+	-	-0.13	0.33	+	-	0.18	0.16	-0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-385.32	795.81	2.14	0.03
0.05	+	-	-0.13	0.33	+	-	0.18	0.17	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	12	-385.34	795.84	2.17	0.03
0.04	+	-	-	0.27	+	-	0.19	0.14	-	-	-0.06	-	-	-	-	-	-	-	-	-	-	-	-	11	-386.43	795.84	2.17	0.03
0.05	+	-	-0.13	0.33	+	0.00	0.18	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-385.35	795.85	2.18	0.03
-0.13	+	-	-	0.16	-	-	0.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-389.70	795.92	2.24	0.03
0.04	+	-	-	0.24	+	-	0.18	0.15	-	-0.05	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-386.53	796.04	2.37	0.03
-0.02	+	-	-	0.19	+	-	0.18	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	10	-387.67	796.16	2.48	0.02
-0.05	+	-	-	0.20	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-389.84	796.21	2.54	0.02

+ for presence, - for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "Δ AIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models; "association time", post-fledging parent-offspring association time; "time start", time of the start of the treatment.

Table 2-S6 following. Adults' vs. nestlings' predation risk analysis excluding 3 black wheatears'nests - Model set obtained after model selection based on ΔAICc ≤ 3.

simple effects													interactions											model information				
(Intercept)	predator type	nest brood size	ln(adult body mass)	maximum longevity	nest type	nest predation rate	re-nesting potential	ln(association time)	ln(daily precipitation)	daily temperature	date of the experiment	time start	predator type: nest brood size	predator type: ln(adult body mass)	predator type: maximum longevity	predator type: nest type	predator type: nest predation rate	predator type: re-nesting potential	predator type: ln(association time)	predator type: ln(daily precipitation)	predator type: daily temperature	predator type: date of the experiment	predator type: time start	df	log Likelihood	AICc	Δ AICc	weight
0.03	+	-	-	0.25	+	-	0.18	0.14	-	-	-	-0.03	-	-	-	-	-	-	-	-	-	-	-	11	-386.65	796.28	2.61	0.02
0.04	+	0.03	-	0.25	+	-	0.18	0.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-386.66	796.30	2.63	0.02
0.06	+	-	-0.12	0.34	+	-	0.25	0.17	-	-	-0.04	-	-	-	-	-	-	+	-	-	-	-	-	13	-384.55	796.46	2.79	0.02
0.04	+	-	-	0.23	+	-	0.18	0.14	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	11	-386.75	796.47	2.80	0.02
0.02	+	-	-	0.25	+	-	0.18	0.14	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	11	-386.75	796.49	2.81	0.02
0.04	+	-	-	0.25	+	0.01	0.18	0.14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-386.77	796.52	2.85	0.02
0.05	+	-	-0.09	0.33	+	-	0.24	0.17	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	13	-384.59	796.53	2.86	0.02
0.04	+	-	-	0.25	+	-	0.18	0.14	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	11	-386.78	796.55	2.87	0.02
0.04	+	-	-	0.25	+	-	0.18	0.14	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-386.79	796.56	2.88	0.02
0.05	+	-	-0.13	0.33	+	-	0.24	0.17	-	-	-	-0.03	-	-	-	-	-	+	-	-	-	-	-	13	-384.63	796.63	2.95	0.02

+ for presence, - for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "Δ AIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models; "association time", post-fledging parent-offspring association time; "time start", time of the start of the treatment.

Table 2-S7. Details on each parameter included in the full models.

parameters	details
visitation rate	the visitation rate was investigated as the number of visitation to the nest per minute; because the recording time of each session varied slightly due to logistic, material or weather issues the number of visitation to the nest scaled by the length of the video was used to calculate the response in visitation rate (i.e. the response variable)
post-fledging parent-offspring association time	number of days offspring stay with their parents after they fledge; obtained from the online version of the Handbook of the Birds of the World [(1)]
body mass	average body mass (in grams) of captured individuals from our populations except for three species (Table 2-S1)
longevity	maximum longevity (in years) obtained from the online version of the Handbook of the Birds of the World [(1)] and Animal Ageing and Longevity database [(2)] (http://genomics.senescence.info/species/)
brood size	the brood size of each experimental nest was noted. The average brood size of successful nests in our population of the specific species and year was used when brood size could not be determined (e.g., narrow natural cavities or open nest difficult to access)
re-nesting potential	the re-nesting potential was given per species and represented the percentage of nests with re-nesting potential within the current breeding season; the latter was assessed based on whether the species is known to have replacement nest(s) after failure or second broods, and on the date of the experiment relative to the end of the breeding season (late in the season the re-nesting chance is low even if the species is known to have replacement)
nest predation rate	value of nest predation rate per species the year the experiment was done, it was estimated from observations of nest failure in our populations; nest predation rate was used as a proximate predictor of predation pressure
nest type	open vs. closed nester; nest type represents the natural vulnerability of the nest and was used as an ultimate predictor of predation pressure
daily precipitation	daily precipitations (in millimetres) recorded by the site taking meteorological measurements the closest to the location each species were studied; obtained from the Andalusian government data base (http://www.juntadeandalucia.es/medioambiente/servtc5/sica/sima_av.jsp); when the daily precipitation equal to zero we added a value of 0.0001 to be able to apply a log transformation
daily temperature	daily temperature (in Celsius degree) recorded by the site taking meteorological measurements the closest to the location each species were studied; obtained from the Andalusian government data base (http://www.juntadeandalucia.es/medioambiente/servtc5/sica/sima_av.jsp)
date of the experiment	number of day since the first nest with egg of the correspondent species and year was found; Min laying date per year per species minus the date of the experiment
time of the start of the treatment	the time was converted into a decimal number using the function TIMEVALUE in excel; it returns time from 0.00 (12:00:00 AM) to 0.999988426 (11:59:59 PM)
adult relative predation risk*	estimate the adult prey's body mass relative to the predator's body mass; based on the assumption that prey profitability for predator increases with prey size and that larger-sized prey are more predated than smaller-sized prey

[1] (Del Hoyo et al. 2011), [2] (de Magalhaes & Costa 2009) *only included in the analysis on adult's predation risk

Table 2-S8. Test of the phylogenetic effect: method and results.

Method:

The phylogenetic dependency among species was controlled by including phylogeny as a random effect in the model in the form of correlation matrix of distances from the root of the tree to the most recent common ancestor between two species. We relied on a recent phyla-wide phylogeny (downloaded from: www.birdtree.org; Jetz *et al.* 2012; Rubolini *et al.* 2015) (Figure 2-S1). The phylogenetic effect was tested using a likelihood ratio test (LRT) where minus two times the difference in log-likelihood between ASReml models with and without the phylogeny is tested against a χ^2 distribution with one degree of freedom (Huelsenbeck & Crandall 1997).

Result from the likelihood ratio test of the phylogenetic effect on ASReml models:

		LRT	df	*p*
adults' vs. nestlings' predation risk analysis	Null model	0.03	1	0.87
	Full model	<0.0001	1	1.00
adults' predation risk analysis	Null model	<0.0001	1	1.00
	Full model	0.01	1	0.92

Table 2-S9. Adults' vs. nestlings' predation risk analysis - Model set obtained after model selection based on ΔAICc ≤ 3.

simple effects													interactions											model information				
(Intercept)	predator type	nest brood size	ln(adult body mass)	maximum longevity	nest type	nest predation rate	re-nesting potential	ln(association time)	ln(daily precipitation)	daily temperature	date of the experiment	time start	predator type: nest brood size	predator type: ln(adult body mass)	predator type: maximum longevity	predator type: nest type	predator type: nest predation rate	predator type: re-nesting potential	predator type: ln(association time)	predator type: ln(daily precipitation)	predator type: daily temperature	predator type: date of the experiment	predator type: time start	df	log Likelihood	AICc	Δ AICc	weight
0.05	+	-	-0.12	0.33	+	-	0.18	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-393.74	810.44	0.00	0.09
0.03	+	-	-	0.25	+	-	0.18	0.14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-395.19	811.18	0.74	0.06
0.05	+	-	-0.12	0.33	+	-	0.24	0.17	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	12	-393.21	811.56	1.12	0.05
-0.02	+	-	-	0.18	+	-	0.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-396.68	812.01	1.57	0.04
0.05	+	-	-0.13	0.33	+	-	0.18	0.17	-	-	-	-0.04	-	-	-	-	-	-	-	-	-	-	-	12	-393.45	812.03	1.59	0.04
0.05	+	-	-0.12	0.35	+	-	0.19	0.17	-	-	-0.04	-	-	-	-	-	-	-	-	-	-	-	-	12	-393.51	812.16	1.72	0.04
0.05	+	-	-0.09	0.33	+	-	0.18	0.17	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	12	-393.53	812.20	1.76	0.04
0.03	+	-	-	0.25	+	-	0.23	0.14	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	11	-394.66	812.28	1.84	0.03
0.05	+	-	-0.12	0.33	+	-	0.19	0.17	-	-0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-393.65	812.44	2.00	0.03
0.05	+	-0.02	-0.13	0.33	+	-	0.18	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-393.69	812.52	2.08	0.03
0.04	+	-	-0.12	0.33	+	-	0.18	0.17	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	12	-393.70	812.53	2.09	0.03
0.05	+	-	-0.12	0.32	+	-	0.18	0.17	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	12	-393.71	812.55	2.11	0.03
0.05	+	-	-0.13	0.33	+	-	0.18	0.17	-0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-393.72	812.57	2.13	0.03
-0.02	+	-	-0.09	0.23	+	-	0.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-395.90	812.60	2.16	0.03
0.05	+	-	-0.12	0.33	+	-	0.18	0.17	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	12	-393.74	812.61	2.17	0.03
0.05	+	-	-0.12	0.33	+	0.00	0.18	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-393.74	812.61	2.17	0.03
0.04	+	-	-	0.27	+	-	0.19	0.14	-	-	-0.06	-	-	-	-	-	-	-	-	-	-	-	-	11	-394.83	812.63	2.19	0.03

+ for presence, - for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "Δ AIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models; "association time", post-fledging parent-offspring association time; "time start", time of the start of the treatment.

Table 2-S9 following. Adults' vs. nestlings' predation risk analysis - Model set obtained after model selection based on ΔAICc ≤ 3.

simple effects													interactions											model information				
(Intercept)	predator type	nest brood size	ln(adult body mass)	maximum longevity	nest type	nest predation rate	re-nesting potential	ln(association time)	ln(daily precipitation)	daily temperature	date of the experiment	time start	predator type: nest brood size	predator type: ln(adult body mass)	predator type: maximum longevity	predator type: nest type	predator type: nest predation rate	predator type: re-nesting potential	predator type: ln(association time)	predator type: ln(daily precipitation)	predator type: daily temperature	predator type: date of the experiment	predator type: time start	df	log Likelihood	AICc	Δ AICc	weight
-0.14	+	-	-	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-399.1	812.6	2.20	0.03
0.03	+	-	-	0.25	+	-	0.17	0.14	-	-	-	-0.04	-	-	-	-	-	-	-	-	-	-	-	11	-394.9	812.8	2.35	0.03
0.04	+	-	-	0.25	+	-	0.18	0.14	-	-0.04	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-394.9	812.8	2.38	0.03
-0.13	+	-	-	0.16	-	-	0.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-398.2	812.9	2.48	0.03
-0.02	+	-	-	0.18	+	-	0.18	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	10	-396.2	813.1	2.66	0.02
0.03	+	0.03	-	0.26	+	-	0.18	0.14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-395.1	813.2	2.72	0.02
0.05	+	-	-0.13	0.33	+	-	0.23	0.17	-	-	-	-0.04	-	-	-	-	-	+	-	-	-	-	-	13	-393.0	813.2	2.74	0.02
0.02	+	-	-	0.25	+	-	0.18	0.14	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	11	-395.2	813.3	2.81	0.02
0.03	+	-	-	0.24	+	-	0.18	0.14	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	11	-395.2	813.3	2.83	0.02
0.05	+	-	-0.12	0.35	+	-	0.25	0.17	-	-	-0.04	-	-	-	-	-	-	+	-	-	-	-	-	13	-393.0	813.3	2.85	0.02
-0.06	+	-	-	0.19	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-398.4	813.3	2.86	0.02
0.04	+	-	-	0.25	+	0.01	0.18	0.14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-395.2	813.3	2.86	0.02
0.03	+	-	-	0.25	+	-	0.18	0.14	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	11	-395.2	813.3	2.89	0.02
0.03	+	-	-	0.25	+	-	0.18	0.14	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-395.2	813.3	2.90	0.02
0.05	+	-	-0.09	0.33	+	-	0.24	0.17	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	13	-393.0	813.4	2.91	0.02

+ for presence, - for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "Δ AIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models; "association time", post-fledging parent-offspring association time; "time start", time of the start of the treatment.

Table 2-S10. Adults' predation risk analysis - Model set obtained after model selection based on ΔAICc ≤ 3.

simple effects													interactions	model information				
(Intercept)	nest brood size	ln(adult body mass)	maximum longevity	nest type	nest predation rate	re-nesting potential	ln(association time)	adult relative predation risk	ln(daily precipitation)	daily temperature	date of the experiment	time start	nest type: nest predation rate	df	log Likelihood	AICc	Δ AICc	weight
0.00	-	-	0.13	-	-	0.16	-	-	-	-	-	-	-	6	-200.41	413.43	0.00	0.03
0.00	-	-	0.18	-	-	0.17	-	-0.13	-	-	-	-	-	7	-199.38	413.58	0.15	0.03
0.20	-	-	0.33	+	-	0.23	0.19	-0.14	-	-	-	-	-	9	-197.21	413.76	0.33	0.02
0.00	-	-	-	-	-	0.17	-	-	-	-	-	-	-	5	-201.67	413.78	0.35	0.02
0.10	-	-	0.21	+	-	0.19	-	-0.13	-	-	-	-	-	8	-198.39	413.84	0.42	0.02
0.10	-	-	0.16	+	-	0.18	-	-	-	-	-	-	-	7	-199.55	413.93	0.50	0.02
0.00	-	-	0.16	-	-0.11	0.16	-	-0.15	-	-	-	-	-	8	-198.47	414.01	0.59	0.02
0.18	-	-	0.26	+	-	0.23	0.18	-	-	-	-	-	-	8	-198.48	414.03	0.60	0.02
0.00	-	-	-	-	-0.11	0.17	-	-	-	-	-	-	-	6	-200.75	414.10	0.68	0.02
0.01	-	-	0.17	-	-	-	-	-	-	-	-	-	-	5	-202.06	414.55	1.12	0.02
0.00	-	-	0.11	-	-0.09	0.15	-	-	-	-	-	-	-	7	-199.88	414.59	1.17	0.02
0.24	-0.12	-	0.37	+	-	0.19	0.23	-0.20	-	-	-	-	-	10	-196.51	414.68	1.26	0.01
0.00	-	-	0.19	-	-	0.16	-	-0.15	-0.09	-	-	-	-	8	-198.82	414.71	1.29	0.01
0.02	-	-	0.22	-	-	-	-	-0.13	-	-	-	-	-	6	-201.15	414.91	1.48	0.01
0.00	-0.09	-	0.17	-	-	0.15	-	-0.16	-	-	-	-	-	8	-198.94	414.95	1.53	0.01
0.00	-	-	-	-	-0.14	0.18	-	-0.10	-	-	-	-	-	7	-200.09	415.01	1.58	0.01
0.03	-0.14	-	0.21	-	-	-	-	-0.19	-	-	-	-	-	7	-200.11	415.04	1.61	0.01
0.00	-	-	0.13	-	-	0.15	-	-	-0.05	-	-	-	-	7	-200.20	415.22	1.80	0.01
0.06	-	-	-	+	-	0.19	-	-	-	-	-	-	-	6	-201.30	415.22	1.80	0.01

+ for presence, - for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "Δ AIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models; "association time", post-fledging parent-offspring association time; "time start", time of the start of the treatment.

Table 2-S10 following. Adults' predation risk analysis - Model set obtained after model selection based on ΔAICc ≤ 3.

simple effects													interactions	model information				
(Intercept)	nest brood size	ln(adult body mass)	maximum longevity	nest type	nest predation rate	re-nesting potential	ln(association time)	adult relative predation risk	ln(daily precipitation)	daily temperature	date of the experiment	time start	nest type: nest predation rate	df	log Likelihood	AICc	Δ AICc	weight
0.00	-0.09	-	0.15	-	-0.12	0.15	-	-0.19	-	-	-	-	-	9	-197.97	415.29	1.86	0.01
0.10	-	-	0.22	+	-	0.18	-	-0.15	-0.08	-	-	-	-	9	-197.97	415.29	1.87	0.01
0.00	-	-	0.15	-	-	0.17	0.05	-	-	-	-	-	-	7	-200.23	415.29	1.87	0.01
-0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-203.51	415.30	1.87	0.01
0.00	-	0.08	0.15	-	-	0.17	-	-0.16	-	-	-	-	-	8	-199.14	415.35	1.92	0.01
0.02	-	-	0.20	-	-0.12	-	-	-0.16	-	-	-	-	-	7	-200.27	415.36	1.94	0.01
0.22	-	-	0.34	+	-	0.24	0.22	-	-	-	-0.10	-	-	9	-198.02	415.38	1.95	0.01
0.00	-	-	0.14	-	-	0.16	-	-	-	-	-0.04	-	-	7	-200.30	415.42	1.99	0.01
0.00	-	0.06	-	-	-	0.17	-	-	-	-	-	-	-	6	-201.41	415.43	2.00	0.01
0.00	-	-	-	-	-	0.18	-	-0.06	-	-	-	-	-	6	-201.41	415.44	2.02	0.01
0.07	-	-	0.19	+	-0.08	0.18	-	-0.15	-	-	-	-	-	9	-198.05	415.45	2.02	0.01
0.24	-	-	0.40	+	-	0.23	0.23	-0.14	-	-	-0.08	-	-	10	-196.90	415.45	2.03	0.01
0.00	-	-	0.17	-	-0.11	0.16	-	-0.17	-0.08	-	-	-	-	9	-198.06	415.46	2.03	0.01
0.00	-	-	0.20	-	-	0.18	0.05	-0.13	-	-	-	-	-	8	-199.21	415.48	2.06	0.01
0.00	-	0.15	-	-	-	0.19	-	-0.15	-	-	-	-	-	7	-200.33	415.48	2.06	0.01
0.10	-0.07	-	0.20	+	-	0.17	-	-0.16	-	-	-	-	-	9	-198.08	415.50	2.08	0.01
0.16	-	-	0.29	+	-	0.24	0.15	-0.16	-0.07	-	-	-	-	10	-196.93	415.51	2.08	0.01
0.00	-0.06	-	-	-	-	0.16	-	-	-	-	-	-	-	6	-201.46	415.53	2.10	0.01

+ for presence, - for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "Δ AIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models; "association time", post-fledging parent-offspring association time; "time start", time of the start of the treatment.

Table 2-S10 following. Adults' predation risk analysis - Model set obtained after model selection based on ΔAICc ≤ 3.

simple effects													interactions	model information				
(Intercept)	nest brood size	ln(adult body mass)	maximum longevity	nest type	nest predation rate	re-nesting potential	ln(association time)	adult relative predation risk	ln(daily precipitation)	daily temperature	date of the experiment	time start	nest type: nest predation rate	df	log Likelihood	AICc	Δ AICc	weight
0.00	-0.02	-	0.13	-	-	0.15	-	-	-	-	-	-	-	7	-200.38	415.58	2.15	0.01
0.16	-	-	0.30	+	-0.07	0.23	0.17	-0.15	-	-	-	-	-	10	-196.97	415.59	2.16	0.01
0.00	-	-	0.19	-	-0.13	0.18	0.08	-0.15	-	-	-	-	-	9	-198.13	415.60	2.17	0.01
0.00	-	-0.01	0.14	-	-	0.16	-	-	-	-	-	-	-	7	-200.40	415.61	2.19	0.01
0.00	-	-	-	-	-	0.17	-	-	-0.05	-	-	-	-	6	-201.50	415.62	2.19	0.01
0.00	-	-	0.13	-	-	0.16	-	-	-	-	-	0.01	-	7	-200.40	415.63	2.20	0.01
0.00	-	-	0.13	-	-	0.16	-	-	-	0.00	-	-	-	7	-200.41	415.63	2.21	0.01
0.00	-	0.13	-	-	-0.12	0.18	-	-0.17	-	-	-	-	-	8	-199.31	415.68	2.26	0.01
0.00	-	-	0.19	-	-	0.16	-	-0.14	-	0.03	-	-	-	8	-199.31	415.69	2.26	0.01
0.29	-0.15	-	0.46	+	-	0.19	0.28	-0.20	-	-	-0.12	-	-	11	-195.87	415.74	2.31	0.01
0.10	-	0.07	0.18	+	-	0.20	-	-0.16	-	-	-	-	-	9	-198.21	415.76	2.33	0.01
0.00	-	-	0.18	-	-	0.17	-	-0.12	-	-	-0.02	-	-	8	-199.36	415.79	2.37	0.01
0.00	-	-	0.18	-	-	0.17	-	-0.13	-	-	-	0.00	-	8	-199.38	415.82	2.40	0.01
0.10	-	-	0.18	+	-	0.19	-	-	-	-	-0.05	-	-	8	-199.39	415.84	2.42	0.01
0.00	-	-	-	-	-	0.17	-	-	-	-0.02	-	-	-	6	-201.63	415.88	2.45	0.01
0.00	-0.11	-	-	-	-0.14	0.15	-	-0.15	-	-	-	-	-	8	-199.41	415.89	2.46	0.01
0.01	-	-	0.14	-	-0.09	-	-	-	-	-	-	-	-	6	-201.64	415.89	2.47	0.01
0.08	-	-	0.14	+	-0.05	0.17	-	-	-	-	-	-	-	8	-199.42	415.91	2.49	0.01
0.09	-	-	0.16	+	-	0.18	-	-	-0.04	-	-	-	-	8	-199.43	415.93	2.50	0.01

+ for presence, - for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "Δ AIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models; "association time", post-fledging parent-offspring association time; "time start", time of the start of the treatment.

Table 2-S10 following. Adults' predation risk analysis - Model set obtained after model selection based on ΔAICc ≤ 3.

simple effects													interactions	model information				
(Intercept)	nest brood size	ln(adult body mass)	maximum longevity	nest type	nest predation rate	re-nesting potential	ln(association time)	adult relative predation risk	ln(daily precipitation)	daily temperature	date of the experiment	time start	nest type: nest predation rate	df	log Likelihood	AICc	Δ AICc	weight
0.00	-0.10	-	0.18	-	-	0.14	-	-0.19	-0.10	-	-	-	-	9	-198.29	415.93	2.51	0.01
0.00	-	-	-	-	-0.11	-	-	-	-	-	-	-	-	5	-202.75	415.94	2.51	0.01
0.00	-	-	-	-	-	0.17	-	-	-	-	0.01	-	-	6	-201.67	415.95	2.52	0.01
0.00	-	-	-	-	-	0.17	-0.01	-	-	-	-	-	-	6	-201.67	415.95	2.52	0.01
0.00	-	-	-	-	-	0.17	-	-	-	-	-	0.00	-	6	-201.67	415.95	2.53	0.01
0.00	-	0.06	0.14	-	-0.11	0.17	-	-0.18	-	-	-	-	-	9	-198.31	415.97	2.54	0.01
0.19	-	-0.06	0.30	+	-	0.23	0.19	-	-	-	-	-	-	9	-198.32	415.97	2.55	0.01
0.23	-0.18	-	0.39	+	-	-	0.20	-0.24	-	-	-	-	-	9	-198.32	415.98	2.55	0.01
0.20	-	0.03	0.32	+	-	0.23	0.18	-0.16	-	-	-	-	-	10	-197.16	415.98	2.56	0.01
0.10	-	-	0.22	+	-	0.20	-	-0.13	-	-	-0.02	-	-	9	-198.35	416.05	2.62	0.01
0.10	-	-	0.22	+	-	0.19	-	-0.14	-	0.02	-	-	-	9	-198.36	416.06	2.63	0.01
0.20	-	-	0.34	+	-	0.23	0.19	-0.14	-	0.01	-	-	-	10	-197.20	416.06	2.63	0.01
0.00	-0.04	-	-	-	-0.11	0.16	-	-	-	-	-	-	-	7	-200.62	416.06	2.64	0.01
0.20	-	-	0.33	+	-	0.23	0.19	-0.14	-	-	-	0.00	-	10	-197.21	416.07	2.64	0.01
0.07	-	-	0.19	+	-	-	-	-	-	-	-	-	-	6	-201.74	416.10	2.67	0.01
0.10	-	-0.03	0.17	+	-	0.18	-	-	-	-	-	-	-	8	-199.52	416.10	2.68	0.01
0.01	-0.07	-	0.16	-	-	-	-	-	-	-	-	-	-	6	-201.75	416.11	2.69	0.01
0.10	-	-	0.21	+	-	0.19	-	-0.13	-	-	-	0.00	-	9	-198.39	416.12	2.69	0.01
0.00	-	-	0.17	-	-0.11	0.16	-	-0.16	-	0.03	-	-	-	9	-198.40	416.14	2.71	0.01
0.10	-	-	0.16	+	-	0.18	-	-	-	-0.01	-	-	-	8	-199.54	416.14	2.72	0.01

+ for presence, - for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "Δ AIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models; "association time", post-fledging parent-offspring association time; "time start", time of the start of the treatment.

Table 2-S10 following. Adults' predation risk analysis - Model set obtained after model selection based on ΔAICc ≤ 3.

simple effects													interactions	model information				
(Intercept)	nest brood size	ln(adult body mass)	maximum longevity	nest type	nest predation rate	re-nesting potential	ln(association time)	adult relative predation risk	ln(daily precipitation)	daily temperature	date of the experiment	time start	nest type: nest predation rate	df	log Likelihood	AICc	Δ AICc	weight
0.03	-	-	-	+	-0.10	0.18	-	-	-	-	-	-	-	7	-200.66	416.14	2.72	0.01
0.10	-	-	0.16	+	-	0.18	-	-	-	-	-	0.01	-	8	-199.54	416.15	2.73	0.01
0.10	-0.01	-	0.16	+	-	0.18	-	-	-	-	-	-	-	8	-199.55	416.17	2.74	0.01
0.00	-	-	-	-	-0.11	0.16	-	-	-0.03	-	-	-	-	7	-200.67	416.17	2.74	0.01
0.18	-	-	0.26	+	-	0.24	0.18	-	-	-0.03	-	-	-	9	-198.41	416.17	2.74	0.01
0.00	-	0.03	-	-	-0.10	0.17	-	-	-	-	-	-	-	7	-200.68	416.18	2.75	0.01
0.16	-	-	0.24	+	-0.03	0.23	0.17	-	-	-	-	-	-	9	-198.42	416.18	2.76	0.01
0.17	-	-	0.25	+	-	0.23	0.17	-	-0.03	-	-	-	-	9	-198.43	416.20	2.77	0.01
-0.01	-0.10	-	-	-	-	-	-	-	-	-	-	-	-	5	-202.89	416.21	2.78	0.01
0.10	-	-	0.25	+	-	-	-	-0.14	-	-	-	-	-	7	-200.70	416.21	2.79	0.01
0.01	-	-	0.22	-	-	-	-	-0.15	-0.09	-	-	-	-	7	-200.70	416.22	2.79	0.01
0.00	-	-	-	-	-0.11	0.17	-	-	-	-0.02	-	-	-	7	-200.70	416.22	2.80	0.01
0.19	-0.03	-	0.27	+	-	0.22	0.19	-	-	-	-	-	-	9	-198.44	416.22	2.80	0.01
0.02	-0.14	-	0.22	-	-	-	-	-0.21	-0.09	-	-	-	-	8	-199.58	416.23	2.80	0.01
0.00	-	-	0.13	-	-0.10	0.17	0.07	-	-	-	-	-	-	8	-199.58	416.24	2.81	0.01
0.00	-	-	-	-	-0.12	0.17	0.02	-	-	-	-	-	-	7	-200.71	416.24	2.81	0.01
0.00	-	-	0.15	-	-0.12	0.16	-	-0.16	-	-	0.02	-	-	9	-198.45	416.24	2.82	0.01
0.00	-	-	-	-	-0.11	0.16	-	-	-	-	0.02	-	-	7	-200.71	416.24	2.82	0.01
0.00	-	-	0.16	-	-	-	-	-	-0.06	-	-	-	-	6	-201.83	416.28	2.86	0.01

+ for presence, - for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "Δ AIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models; "association time", post-fledging parent-offspring association time; "time start", time of the start of the treatment.

Table 2-S10 following. Adults' predation risk analysis - Model set obtained after model selection based on ΔAICc ≤ 3.

simple effects													interactions	model information				
(Intercept)	nest brood size	ln(adult body mass)	maximum longevity	nest type	nest predation rate	re-nesting potential	ln(association time)	adult relative predation risk	ln(daily precipitation)	daily temperature	date of the experiment	time start	nest type: nest predation rate	df	log Likelihood	AICc	Δ AICc	weight
0.00	-	-	0.16	-	-0.11	0.16	-	-0.15	-	-	-	0.00	-	9	-198.47	416.29	2.86	0.01
0.18	-	-	0.26	+	-	0.23	0.18	-	-	-	-	0.01	-	9	-198.48	416.30	2.88	0.01
0.00	-	-	-	-	-0.11	0.17	-	-	-	-	-	0.01	-	7	-200.74	416.30	2.88	0.01
0.05	-0.16	-	0.28	-	-	-	0.11	-0.21	-	-	-	-	-	8	-199.65	416.36	2.93	0.01
0.05	-0.16	-	0.26	-	-0.14	-	0.12	-0.25	-	-	-	-	-	9	-198.51	416.37	2.95	0.01
0.00	-0.11	-	-	-	-	0.16	-	-0.11	-	-	-	-	-	7	-200.80	416.43	3.00	0.01

+ for presence, - for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "Δ AIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models; "association time", post-fledging parent-offspring association time; "time start", time of the start of the treatment.

Figure.2-S1. Phylogenetic tree for the 12 species studied (based on the full tree from Jetz et al. 2012; Ericson backbone phylogeny (www.birdtree.org)).

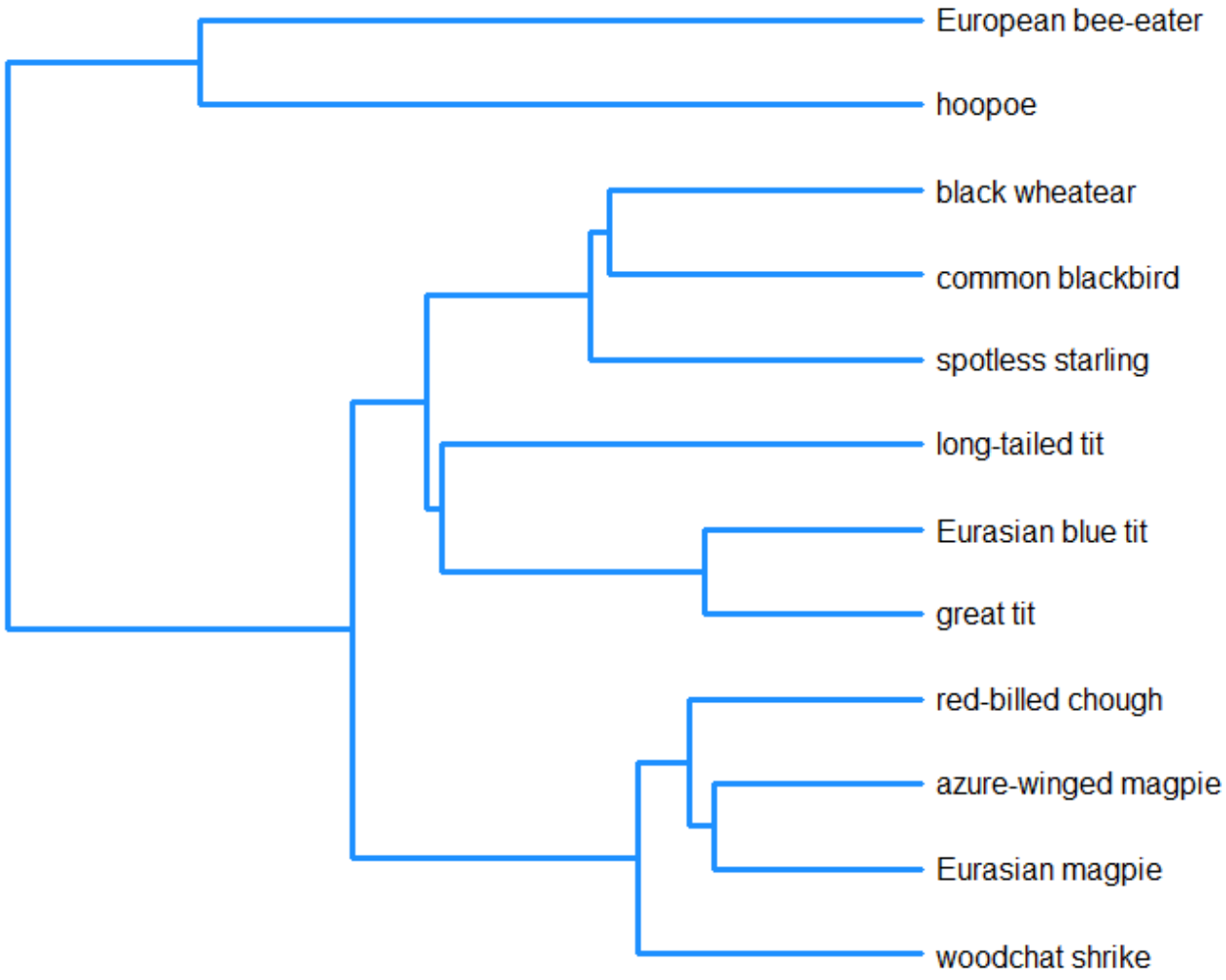


Figure.2-S2. Visitation rate (per minute) (average ± 2se) per treatment and per session for the 12 species studied. The number of nests investigated is presented in parenthesis after the name of the species (N). Note: 4 species reacted to the control treatment: common blackbird, bee-eater, red-billed chough and Eurasian Magpie.

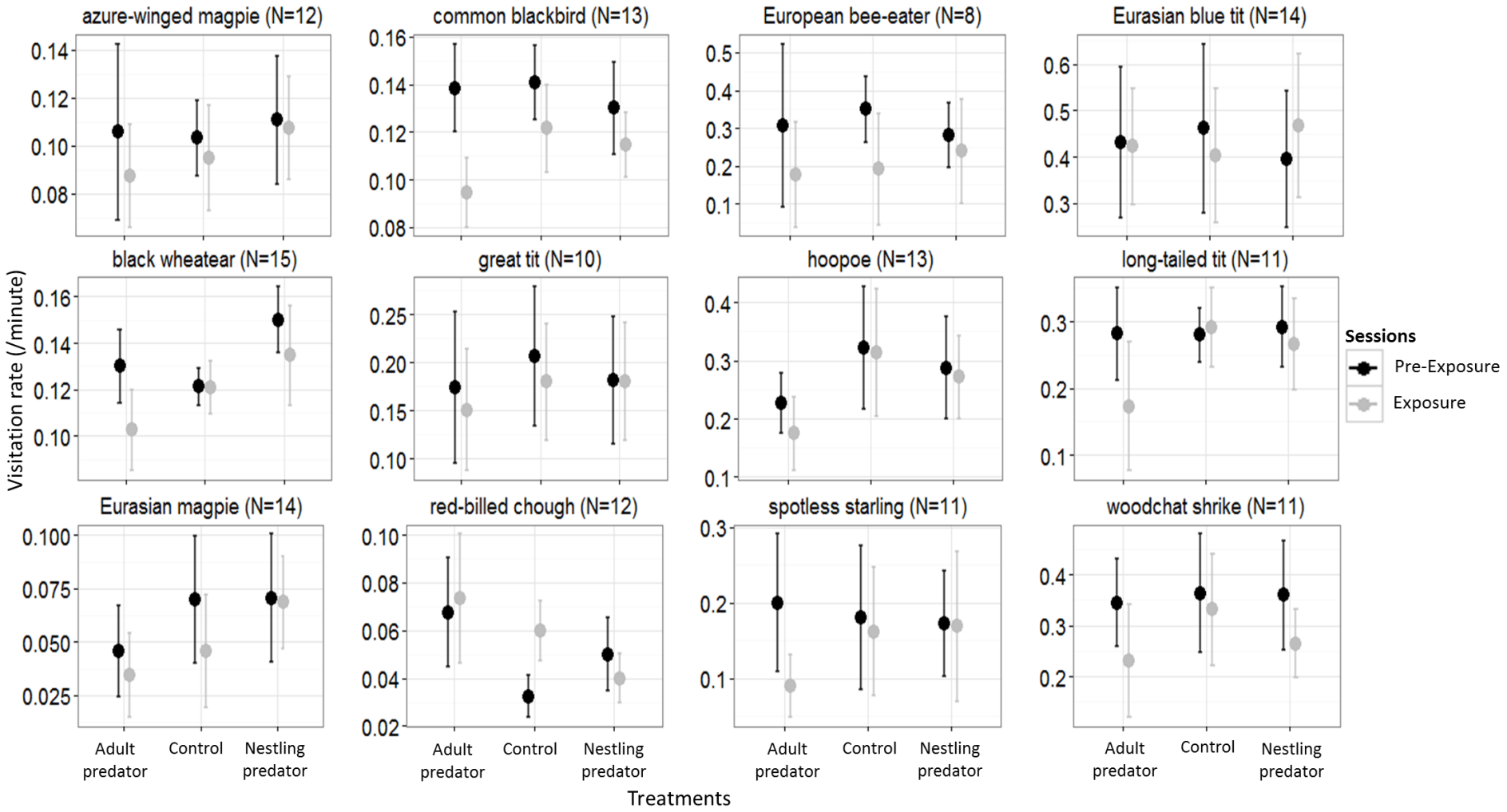


Figure 2-S3. Overall species differences (average ± 2se) between the pre-exposure and exposure session of each treatment on the visitation rate (per minute).

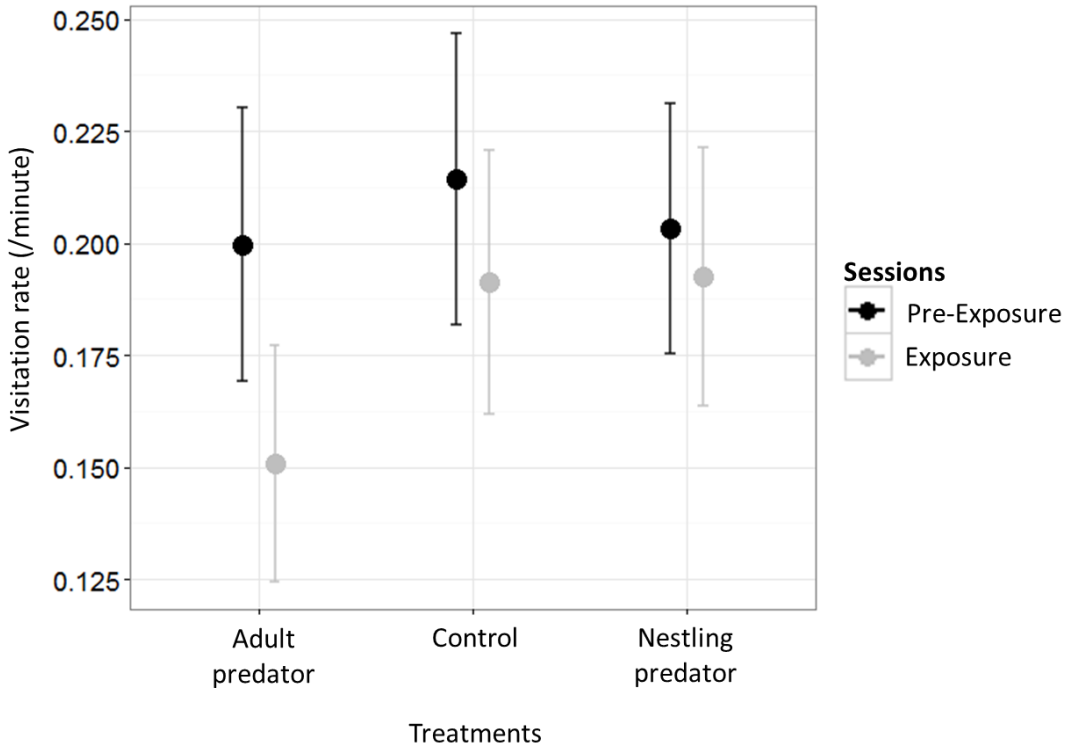
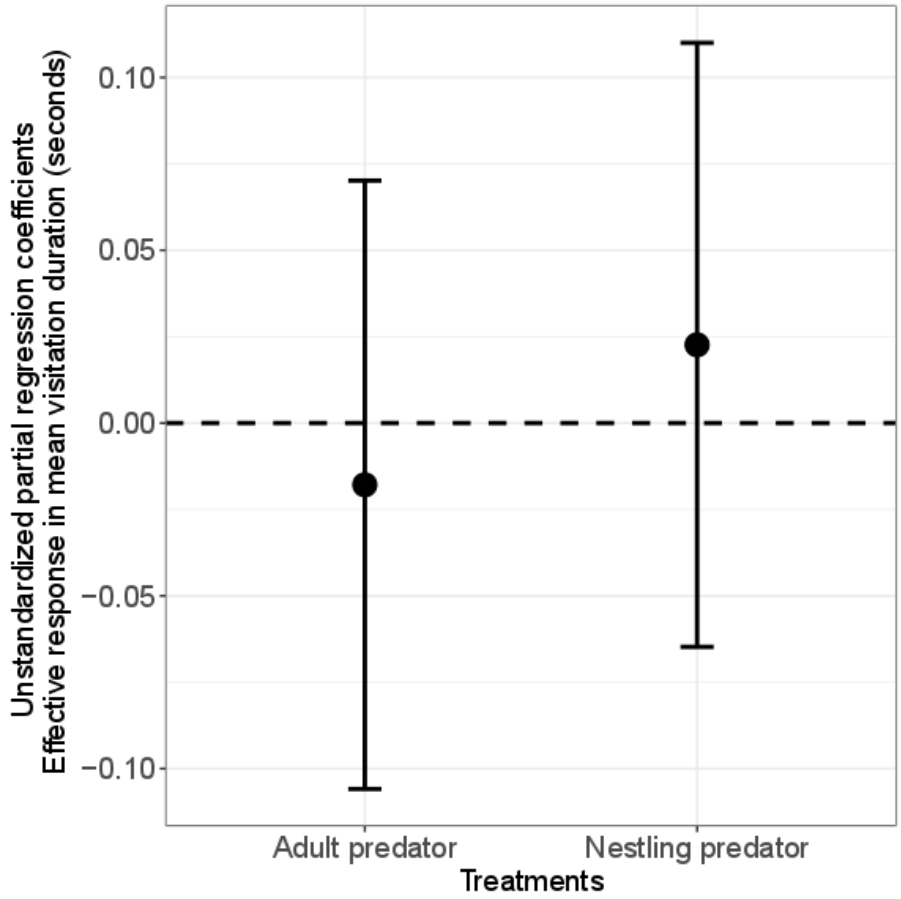


Figure 2-S4. Difference in parental mean visitation duration (seconds) between adult and nestling predator treatments (unstandardized partial regression coefficients and 95% CI).



The dashed line represents equality of response between control and predators treatments. If the 95%CI overlaps this dashed line (includes the value of zero), it means that the responses to the predator and the control treatments do not differ significantly. The further away from this line the higher the response. Positive values indicate an increase in response and negative values a decrease.

Figure 2-S5. Correlation between the response in visitation rate (per minute) and the response in another parental investment behavior, the mean visitation duration (seconds), for the adult and nestling predator treatments. The dashed lines represent equality of response between control and predator treatments. The further away from those lines the higher the response. Positive values indicate an increase in response and negative values a decrease.

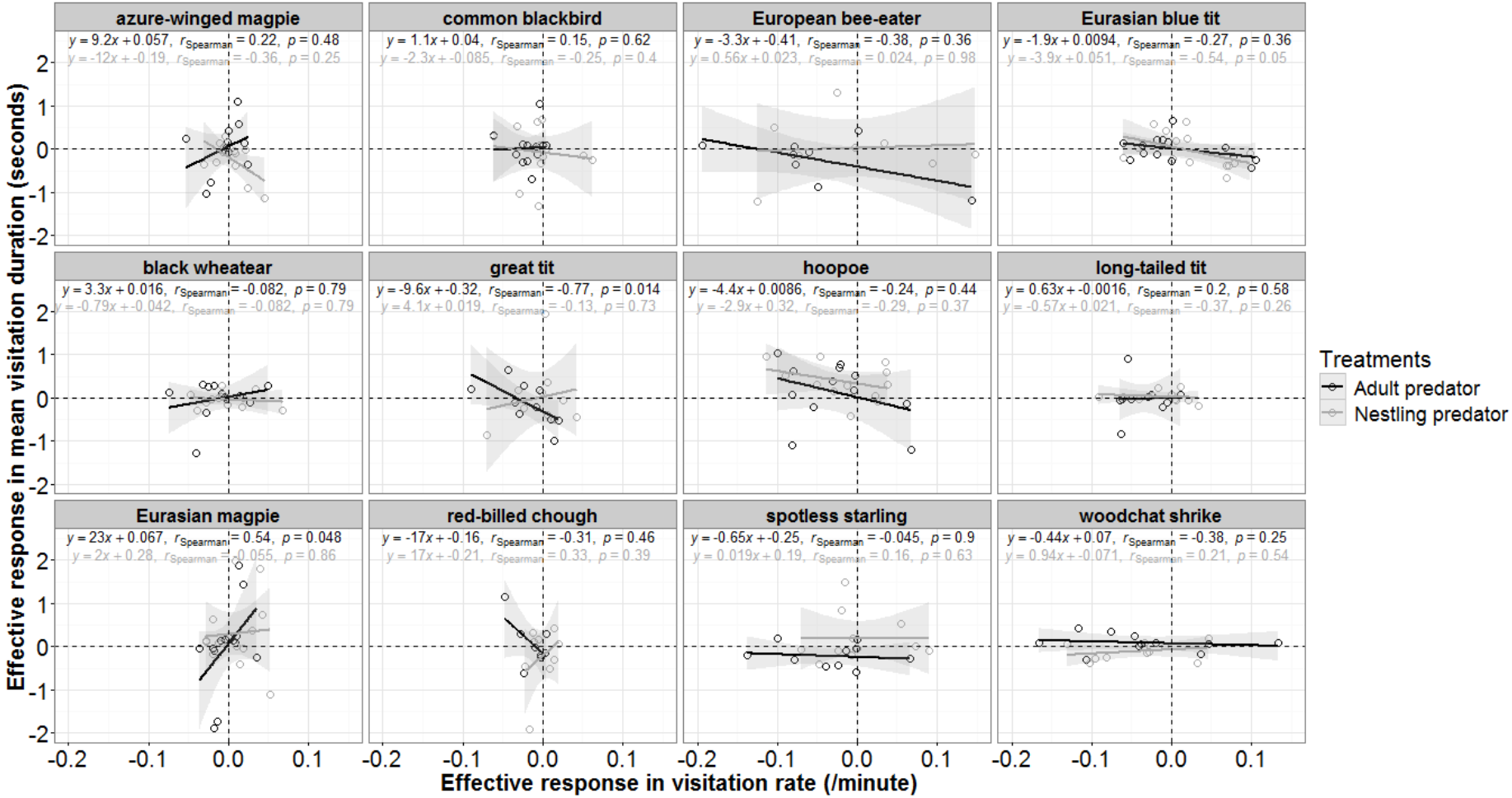
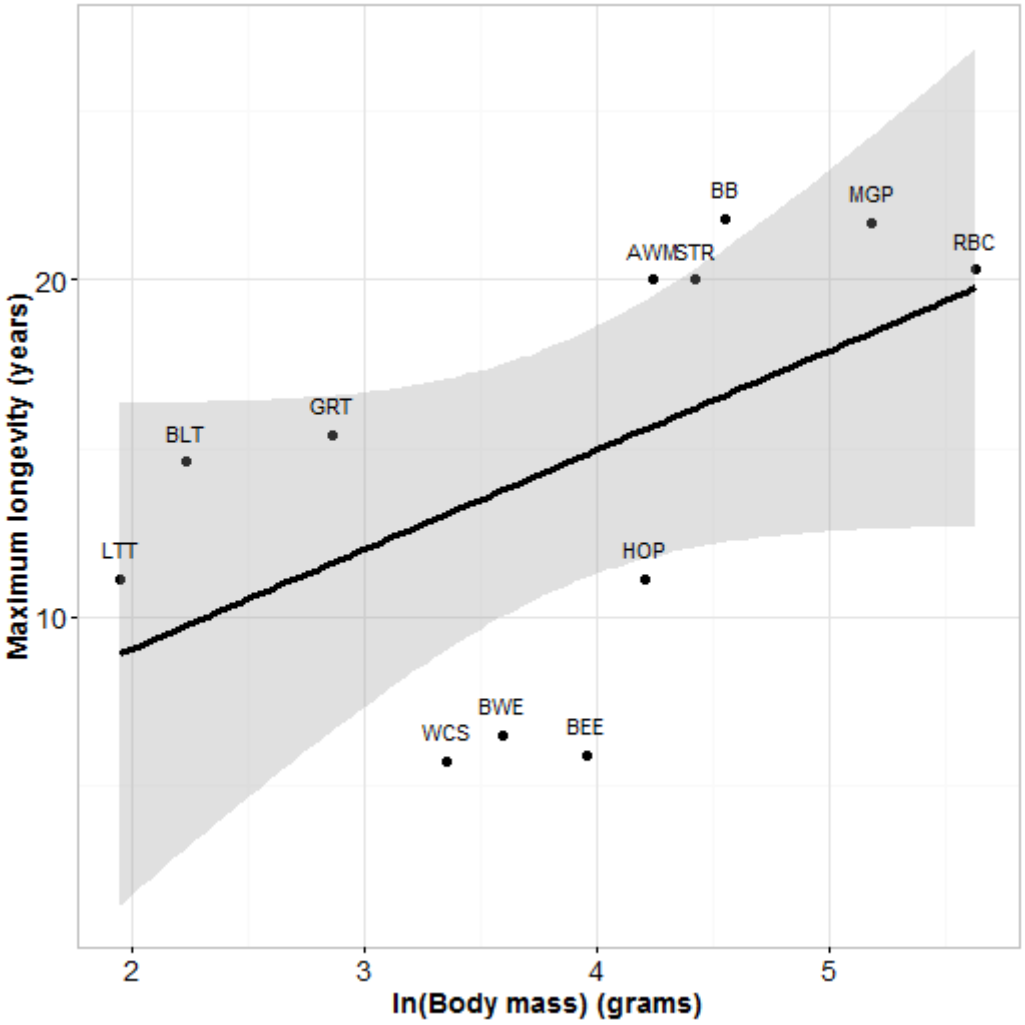
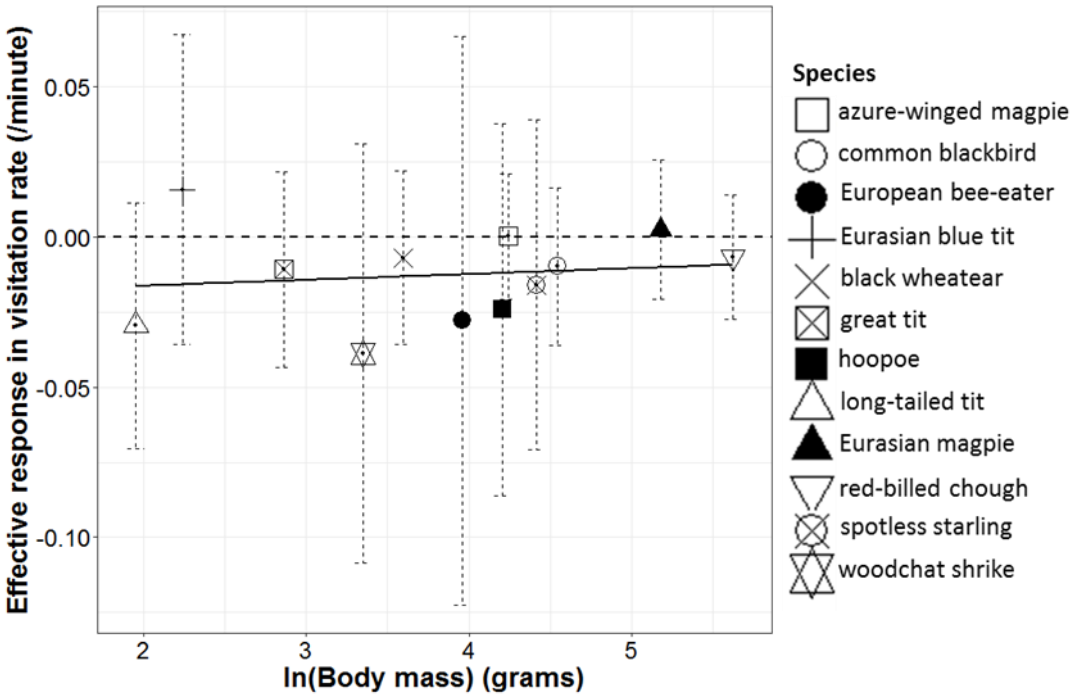


Figure 2-S6. Correlation between maximum longevity and body mass (natural logarithm). Slope = 3.01, rSpearman = 0.71, p < 0.0001. Note, while correlation between body mass and longevity is high it was not regenerating collinearity issues (maximum VIF in full models < 2.8).



AWM: azure-winged magpie, BB: common blackbird, BEE: European bee-eater, BLT: Eurasian blue-tit, BWE: black wheatear, GRT: great tit, HOP: hoopoe, LTT: long-tailed tit, MGP: Eurasian magpie, RBC: red-billed chough, STR: spotless starling, WCS: woodchat shrike

Figure 2-S7. Average change (controlled for the predator treatments effect) in parental responses in visitation rate (per minute) to increased risks of predation relative to adult body mass (mean ± SD).



The dashed line represents equality of response between control and predator treatments. The further away from this line the higher is the response. Positive values indicate an increase in response and negative values a decrease. In (a) and (b), for visual simplification we graphically represented the species' means, but the analysis was run on the full dataset.

- Chapter 3 -

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Interspecific variation in the combination between juvenile survival and longevity: its relationship with life-history, ecology and parental care mode

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Abstract

According to the classical evolutionary theory of aging, juvenile survival and longevity should be positively correlated. However, recent theoretical studies challenged this prediction and propose that any type of association could exist under specific circumstances. Yet, we lack comparative studies assessing survival across different life stages and little is known about the conditions that link with the different juvenile survival-longevity associations. Here, we investigated how life-history, ecological and social factors associated with juvenile survival, longevity and with deviations from the pattern expected under the classical theory in 204 bird species. The overall trend concurred with the classical theory of a positive correlation between juvenile survival and longevity. However, most species (78%) fell out of the 95% CI of the juvenile survival-longevity regression. As hypothesized, a slow life-history correlated with a high juvenile survival and a long lifespan. In contrast to species following predicted relationship, species that deviated from the expected juvenile survival-longevity regression are characterized by low exposure to predators, slow life-history, nocturnality, habitat generalism and uniparental care, independent of the direction of the deviation. In species that displayed non-consistent deviations (i.e. fully contrasting with a positive relationship), however, its direction was important. Species that expressed high juvenile but short lifespan live in stable environments, breed cooperatively, have precocial young and a specialized diet, while the reverse was partly true for species with a low juvenile but a long lifespan. Overall, these results highlight that different ecological and life-history conditions associated with different combinations of juvenile survival and longevity in birds and underpin the importance of considering age-specific survival in evolutionary studies.

Key Words: Comparative method, first-year survival, life-history evolution, maximum longevity.

3.1 Introduction

In vertebrates, lifespan varies considerably across species, ranging from a few months to over 100 years. Although lifespan is an important factor shaping life-histories (Roff 1992; Stearns 1992), age-specific survival may provide more comprehensive insights into life-history evolution. For example, turtles suffer from high juvenile mortality, and accordingly females lay many eggs in each reproductive event, but still, turtles are exceptionally long-lived. Both theoretical (Cole 1954; Williams 1966; Promislow & Harvey 1991; Roff 1992; Charlesworth 1994) and empirical studies (fishes: Reznick, Bryga & Endler 1990; birds: Martin 2002; mammals: Kraus *et al.* 2005), support the importance of age-specific survival, which can explain unusual combination of life-history traits such as the long gestation period and low number of young but early maturation found in caviomorph rodents (Kraus *et al.* 2005). However, while inter-specific variation in longevity is well investigated (Carey & Tuljapurkar 2003; Møller 2006; Wasser & Sherman 2010; Healy *et al.* 2014; Valcu *et al.* 2014), the factors that influence survival early on in life and its relationship to longevity remain unclear (Maness & Anderson 2013).

Comparative studies in vertebrates showed that an increased longevity is associated with a slow life history pace (Roff 1992; Charlesworth 1994), a low number of co-occurring predators of adults (Valcu *et al.* 2014), the ability to fly (Healy *et al.* 2014) or activity during the period of day with the lowest predation risk (Healy *et al.* 2014). Moreover, juveniles have a high survival in species with a long nestling period (Martin 2014), in species with low reproductive allocation (Skutch 1985; Ricklefs 2000b) or prolonged post-fledging care (Grüebler & Naef-Daenzer 2010), or when having a prolonged association with the parents beyond independency (i.e. family-living species, see Drobniak *et al.* 2015) (Griesser, Nystrand & Ekman 2006a; Robinson *et al.* 2010). Thus, while reduced costs of reproduction and a lower extrinsic and intrinsic mortality favor long lifespan, increased parental allocation per offspring and prolonged association beyond independency increase offspring survival.

Classical evolutionary theory of aging assumes that extrinsic mortality experience by young adult individuals (approximated in this study by the first-year survival rate and referred as juvenile survival) influences the proportion of adult individuals that reaches old age. It predicts that in population with lower extrinsic mortality (i.e. high juvenile survival), more individuals survive to older ages (Williams 1957; Charlesworth 1994; Ricklefs 1998; Kirkwood 2002). Hence, according to this classical theory juvenile survival and longevity should be positively correlated. Evidences that in a large range of animals adaptations that reduce extrinsic mortality are linked to increased longevity also comfort this prediction (Kirkwood 2002). Nevertheless, species can deviate from this expected relationship and have a low chance of survival early in life but a long lifespan or vice versa (Abrams 1993; Reznick *et al.* 2004; Chen & Maklakov 2012; Shokhirev & Johnson 2014), yet, it remains unclear what associate with such deviations.

The positive correlation between juvenile and adult survival can be broken up if different selective factors influence different life stages (Lack 1966; Sullivan 1989). Juveniles have a smaller body size than adults and are therefore more susceptible to predation (Caro 2005; Valcu *et al.* 2014). Also, juvenile survival may be low in species that live in complex niches, have elaborated foraging technics or a specialized diet thus, for which offspring require more time to acquire adult skill levels (Heinsohn 1991; Bautista, Tinbergen & Kacelnik 2001). In contrast, only adults are affected by costs of reproduction, which may reduce their lifespan directly due to costs of reproduction, or indirectly, for instance through increased exposure to predators as a consequence of increased foraging effort (Zarybnicka, Korpimaki & Griesser 2012).

Here we used a comparative approach to understand interspecific variation in juvenile survival (first-year survival) and maximum longevity in 204 bird species. We used phylogenetic controlled linear mixed models to examine the relationship between juvenile survival and longevity with life-history, ecological and social parameters. Then we used the same analytical approach to investigate why certain species deviate from the positive relationship between

juvenile survival and longevity predicted under the classical theory of aging, and why some of them in a way that fully contradict the latter (i.e. with inversely correlated juvenile survival and longevity). In other words, we address the question of whether there are consistent differences between species with different juvenile survival-longevity combination in terms of their life history, ecology or social traits.

3.2 Materials and Methods

3.2.1 SURVIVAL DATA

We collected data on juvenile survival and maximum longevity for 293 bird species from 20 taxonomic orders and 74 families (Figure 3-S1). Juvenile survival was measured as the proportion of fledglings that survive their first year of life and was considered a proxy of extrinsic mortality. Whenever possible we used records of maximum longevity from the wild. Maximum longevity was for 19 species of unknown origin (from captivity or the wild), but earlier studies showed that longevity records in captivity highly correlate with the one from the wild (Wasser & Sherman 2010; Valcu *et al.* 2014) and thus, we included those longevity data of unknown origin. As longevity records are influenced by the research effort (Valcu *et al.* 2014), we included the independent number of Web of Science records per species in our analyses (http://apps.webofknowledge.com).

3.2.2 LIFE-HISTORY, ECOLOGY AND SOCIAL PARAMETERS

We compiled data on life-history, ecological and social parameters that may influence juvenile and longevity. We could find data for the 20 parameters listed in Table 3-1 for 204 of the 293 species (Figure 3-S2). Thus, we used for descriptive analyses 293 species while for the mixed models 204 species. Data were gathered from the online version of the Handbook of the Birds of the World (Del Hoyo *et al.* 2011), the Birds of North America (Poole 2005), the Handbook of

Australian, New Zealand and Antarctic Birds (Higgins *et al.* 1996-2006), the Handbook of Southern Africa (Maclean & Robert 1985), the Australian Birds and Bats Banding Scheme (Commonwealth of Australia 2014) and Animal Ageing and Longevity database (http://genomics.senescence.info/species/; de Magalhaes & Costa 2009).

Table 3-1. Description and prediction of the parameters investigated in this study.

	parameter's name	description	prediction
life-history	adult body mass*	mean adult body mass (g)	larger body size confers better ability to cope with temporary food shortages, climatic fluctuations and extreme weather than smaller body size; large body size may associate with higher first-year survival and longer lifespan
	incubation period*	number of days from laying to hatching	longer incubation period may associate with higher first-year survival and longer lifespan
	nestling period*	number of days from hatching to fledging	longer nestling period may associate with higher first-year survival and longer lifespan
	annual parental investment*	body-mass scaled annual reproductive investment [1]	higher parental investment may associate with lower first-year survival and shorter lifespan
	chick development mode	precocial vs. non precocial; semi-altricial or semi precocial species were categorized as non precocial	precocial species should have lower first-year survival but longer lifespan because of lower parental care after hatching while the opposite is expected for altricial species
ecological	sedentariness	resident vs. migratory; based on the species maximum movement; sedentary species or with local movement were categorized as resident and the one with regional or inter-continental movement as migratory	costs associated with migration could translate into lower first-year survival and shorter lifespan in migratory than in non-migratory species
	period of activity	diurnal vs. nocturnal; crepuscular species were categorized as nocturnal	species that are active at night are likely to be harder for predators to detect and predators are more scarce at night thus, nocturnal species might have higher first-year survival and live longer than diurnal species
	nest predation risk*	based on both most commonly used nest location and nest type; ordinally ranked: 1 = inaccessible nests in cavities, 2 = open nests in cliffs or tree, 3 = open nest in shrub-layer or the ground [2]	nest predation risk may alter the developmental phase of the nestling and the reproductive effort of the parents which may affect first-year survival and longevity; greater nest predation risk may associate with lower first-year survival and shorter lifespan
	foraging exposure*	level of exposure to predators during foraging time based on most commonly used foraging area; ordinally ranked: 1 = pelagic species, 2 = aerial foragers, 3 = terrestrial foragers	pelagic or aerial forager should have lower predation risk and be more capable of escaping from predators than species that feed on the ground; first-year survival and longevity may be reduced in the latter more than in the formers
	caloric content of food*	energy content of the food in kcal/100g [3]	food calory content can influence the energy available for maintenance; high calory diet may associate with higher first-year survival and longer lifespan
	fibre content of food*	fiber food content in g/100g [3]	food fiber content can influence digestion efficiency and thus the level of resource acquired and health; high fiber diet may associate with higher first-year survival and longer lifespan
	foraging cost*	level of energy demand for foraging based on most commonly used foraging technics; ordinally ranked: 1 = sit and wait hunters, 2 = swimming or short perch & short flights, 3 = aerial or under water foraging, 4 = terrestrial or gleaners [4]	species with highly energetically demanding foraging strategies may have lower first-year survival and shorter lifespan than species with less energetically demanding technics

	diet specialization	specialist (only one diet class) vs. generalist (more than one diet class)	a change in the food availability can have higher costs for specialist than generalist species as the later can deviate to other food resources; specialisation may associate with lower first-year survival and shorter lifespan
	habitat specialization	specialist (only one habitat type) vs. generalist (more than one habitat type) [5]	a change in habitat availability can have higher costs for specialist than generalist species as the latter can occupy other habitat types; specialisation is predicted to associate with lower first-year survival and shorter lifespan
	MGS duration*	mean duration of the growing season in months [6] (i.e. month(s) of the year in which weather conditions (i.e. temperature, rainfall) allow significant plant productivity)	a short growing season implies changes in environmental conditions over the year, thus MGS duration can be seen as a proxy of environemental variability; less variable environments (long growing season) may associate with higher first-year survival and longevity than highly variable environment (short growing season)
	region	breeding distribution range: northern or southern hemisphere, both hemispheres, island	southern hemisphere and island species may have higher first-year survival and longer lifespan compared to northern hemisphere species
	vegetation cover*	cover of woody vegetation in habitat (%)	more open habitats provide less visual cover than habitats dense in vegetation, increasing the risk of being killed; thus, low vegetation density may associate with lower first-year survival and shorter lifespan
	N avian predators*	number of sympatric adult's or independent juveniles' predator species [7]	a higher number of predators increases the risk of being predated; higher number of predators may associate with a lower first-year survival and shorter lifespan
social	parental care mode	uniparental, biparental, cooperative breeding	the presence of additional carer can reduce survival risk on young and survival cost on the other carer(s); biparental and cooperative breeding species may have higher first-year survival and longer lifespan than uniparental species
	social system	family living (offspring remain at least 50 days beyond nutritional independency with parents) vs. non-family living [8]	species with prolonged post-fledging parental care or having a prolonged association with the parents beyond independency, as in family-living species, may have higher first-year survival and shorter lifespan

Because experience (e.g., foraging, competition, reproductive strategies, anti-predation behaviors) differs between young individuals (inexperienced) and adults (experienced), we also assumed each of the abovementioned parameters to diferentially influence first-year survival and longevity, and potentially explain variation in first-year survival/longevity relationships.
* Included in the PCA (Table 3-2). The other parameters are categorical variables. [1] (Sibly *et al.* 2012), [2] (Martin & Li 1992; Martin 1993), [3] (Isler & van Schaik 2006), [4] (Schmidtn.K 1972), [5] (IUCN 2007), [6] (Botero & Rubenstein 2012), [7] (Valcu *et al.* 2014), [8] (Drobniak *et al.* 2015)

3.2.3 STATISTICAL ANALYSES

3.2.3.1 General procedure

All statistical analyses were performed in R version 3.2.0 (R Core Team 2015). We used phylogenetic controlled mixed models in ASReml-R (VSN International, Hempstead, U.K.; Butler 2009) to control for the phylogenetic dependency among species. We included phylogeny as

random effect in the model in the form of correlation matrix of distances from the root of the tree to the most recent common ancestor between two species. We tested the phylogenetic effect with a likelihood ratio test where 2 times the difference in log-likelihood between the model with and without the phylogeny is tested against a χ^2 distribution with one degree of freedom (Huelsenbeck & Crandall 1997). To account for phylogenetic uncertainty, all *asreml* models were run with 300 different phylogenetic trees obtained from www.birdtree.org (Jetz *et al.* 2012). We averaged the estimates from the 300 models and present the averaged estimates, their 95% CI and the Fs_{300} (proportion of trees for which the term was $p < 0.05$). A conditional Wald F-test was used to evaluate the significance of fixed effects. All continuous variables were centered (around the mean) and scaled (by the standard deviation) for the statistical analyses to allow direct comparison of the model estimates (Schielzeth 2010), but we present raw data in the figures. We checked for the assumptions of normally distributed and homogeneous residuals by visually inspecting histograms and qq-plots of the residuals as well as residuals plotted against fitted values.

We performed a principal component analysis (PCA) with varimax rotation including all 12 continuous predictors to reduce their collinearity (Dormann *et al.* 2013), and extracted 7 PC's given in Table 3-2. Prior to the PCA, the distribution of these predictors were checked graphically and if necessary transformed to obtain a more symmetrical distributions, and subsequently centered and scaled as previously described. Full mixed models included the 7 PC's, the 8 categorical variables from Table 3-1, and as covariates research effort (log transformed) and body mass (log transformed) to control for allometry (Møller 2006; Valcu *et al.* 2014). Since the life-history pace PC was loaded by adult body mass (Table 3-2) and therefore partially controlled for allometry, we only included as body-mass covariate the residuals from a linear model between natural logarithm adult body mass and the life-history pace component. This way the presence of both the life-history pace PC and the residual body mass in the model allow to fully control for allometry.

Table 3-2. Results of the Principal Component Analysis (PCA) with varimax rotation on the 12 continuous predictors.

			life-history pace	**exposure to predators**	**food fiber**	**nest predation risk**	**N avian predators**	**foraging cost**	**MGS duration**		
category	transformation		1	7	2	6	3	5	4	h2	u2
life-history	ln	adult body mass	**0.90**	-0.25	-0.08	0.13	-0.01	-0.17	-0.12	0.95	0.055
	none	annual parental investment	**-0.89**	0.14	-0.17	0.13	0.14	-0.05	-0.02	0.87	0.128
	sqrt	incubation period	**0.76**	-0.35	0.23	-0.03	-0.10	-0.28	-0.04	0.84	0.160
	none	nestling period	0.51	0.04	0.44	-0.58	-0.13	0.01	0.20	0.85	0.147
ecological	none	nest predation risk	0.05	-0.10	-0.12	**0.94**	-0.12	0.09	-0.07	0.93	0.067
	none	foraging cost	-0.17	0.02	-0.11	0.08	-0.07	**0.96**	-0.05	0.98	0.020
	none	calorie content of food	0.15	0.49	0.62	0.02	0.44	0.01	-0.01	0.83	0.165
	ln	fiber content of food	-0.11	0.16	**-0.89**	0.22	-0.01	0.15	-0.10	0.92	0.085
	none	foraging exposure	-0.30	**0.86**	-0.04	-0.01	0.04	-0.02	0.00	0.83	0.166
	sqrt	vegetation cover	-0.21	**0.85**	-0.01	-0.13	-0.08	0.05	0.11	0.80	0.201
	sqrt	N avian predators	-0.18	-0.03	0.08	-0.07	**0.95**	-0.05	0.00	0.95	0.053
	none	MGS duration	-0.06	0.08	0.08	-0.11	-0.01	-0.05	**0.98**	0.99	0.008
		SS loadings	2.68	1.94	1.5	1.34	1.15	1.07	1.05		
		cumulative variance explained (%)	22	39	51	62	72	81	89		

We considered coefficients of correlation greater than 0.7 or less than -0.7 to be high loadings.

3.2.3.2 Correlates of juvenile survival and longevity

To identify which factors correlate with juvenile survival and longevity, we ran two phylogenetically controlled linear mixed-effects models including the same life-history, ecological and social predictors. We fitted in both cases the full models (see above) and centered (around the mean) and scaled (by the standard deviation) each response variable in order to be able to compare the influence of the each predictors on both response variables, juvenile survival and longevity (Schielzeth 2010). For the latter reason we also did not perform a model selection so that the same set of predictors were present in the two model outputs to compare.

3.2.3.3 Unexpected combination of juvenile survival and longevity

We run two separate analyses to understand the association of species-specific traits with combinations of juvenile survival and longevity that deviate from the classical theory of ageing (positive correlation between juvenile survival and longevity). The first analysis included all species where juvenile survival and longevity were not well correlated (labelled unexpected species hereafter, see below; Table 3-3 and Figure 3-1). The second analysis included only the latter species with combinations of juvenile survival and longevity fully contradicting the classical theory of aging (i.e. negatively linked; labelled non-consistent species hereafter, see below; Table 3-3 and Figure 3-1).

We estimated orthogonal residuals (allowing for errors in both X and Y) from a *Deming* regression of longevity on juvenile survival (N = 293 species) using the *Deming* function in the *MethComp* package (Carstensen *et al.* 2013) to evaluate the degree of deviation from the expected positive relationship between juvenile survival and longevity. We could assume a ratio of the variance of *y* relative to *x* of one since both variables were scaled (by the standard deviation). High absolute residual values indicate combinations of juvenile survival and longevity that largely differ from the one expected under the classical theory of aging (positive correlation

between juvenile survival and longevity). Species outside the confidence interval of the estimated Deming regression slope were categorized as "unexpected species" as their deviations were outside the range of combinations between juvenile survival and longevity that significantly fitted the classical theory (Figure 3-1, 3-S3 and Table 3-3). We separated these species into consistent or non-consistent species using the median of juvenile survival and longevity (Figure 3-1 and Table 3-3). Non-consistent species had a low juvenile survival but a long lifespan, or vice versa.

Table 3-3. Description of the species categorization based on their juvenile survival-longevity combination.

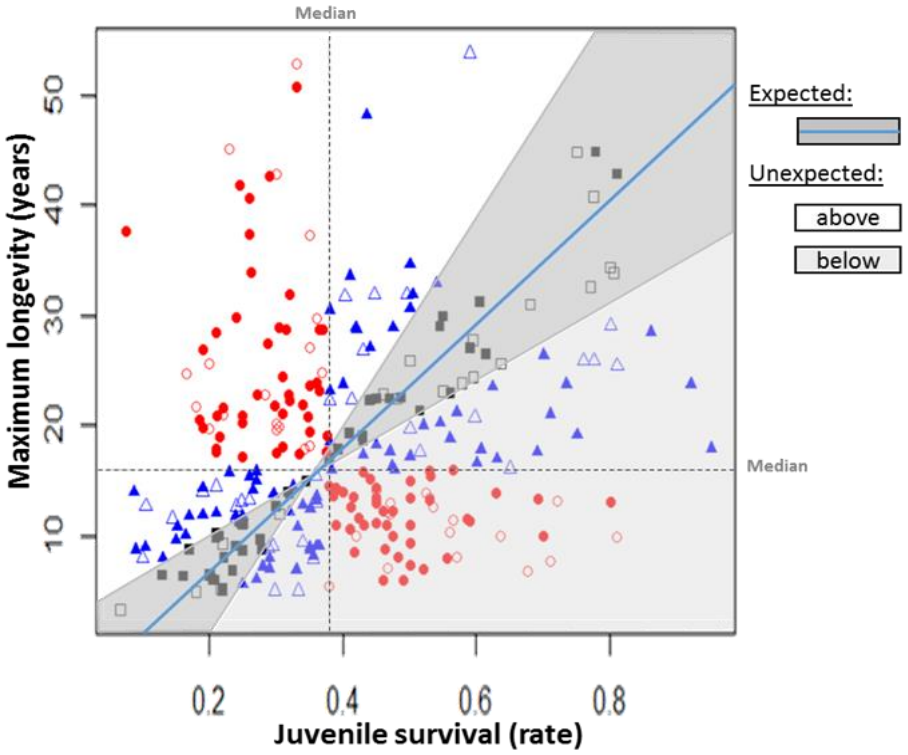
Label	Technical description	Biological description
expected	species inside the 95% confidence interval of the estimated *Deming* regression*	species with combinations of juvenile survival and longevity that fully fit the expected positive correlation under the classical theory of aging [1]
unexpected	species outside the 95% confidence interval of the estimated *Deming* regression*; includes consistent and non-consistent species (see below)	species with combinations of juvenile survival and longevity that deviate from the expected positive correlation
consistent	species outside the 95% confidence interval of the estimated Deming regression* plus, above both the median of juvenile survival and longevity, and below both the median of juvenile survival and longevity	with combinations of juvenile survival and longevity outside the range of a full fit with the expected positive correlation [1] but still with combinations of juvenile survival and longevity consistent with the classical theory [1](i.e. unexpectedly high juvenile survival and long lifespan or unexpectedly low juvenile survival and short lifespan)
non-consistent	species outside the 95% confidence interval of the expected Deming regression* plus, above the median of juvenile survival and below the median of longevity, and below the median of juvenile survival and above the median of longevity	species with combinations of juvenile survival and longevity outside the range of a full fit with the expected positive correlation [1] but with combinations of juvenile survival and longevity that fully contradicting the classical theory [1] (i.e. with unexpectedly high juvenile survival and short lifespan or unexpectedly low juvenile survival and long lifespan)

* *Deming* regression of maximum longevity on juvenile survival (N = 293 species), [1] (Williams 1957)

We fitted phylogenetically controlled linear mixed-effects models on the absolute orthogonal residuals from the relationship between longevity and juvenile survival (representing the degree of deviation) using all unexpected species and using only non-consistent species. We used the same set of predictors and covariates as in the full models of juvenile survival and longevity. The degree of deviation from the juvenile survival-longevity regression may correlate

with different factors depending on the direction of the residual. Thus, we included the residual sign (i.e., below or above the regression line; Figure 3-1) as a factor in the analyses and in interaction with each predictor. For both models, we used a backward model selection process. We successively removed non-significant effects prioritizing the interactions and following with the simple effects, based on the AICc criterion, using model.sel function from the MuMIn package (Barton 2013) and a ΔAICc (i.e., $AICc_{included} - AICc_{excluded}$) > 2 as threshold (Burnham & Anderson 2011).

a)



Blue line: predicted *Deming* regression line done on the set of 293 species, d*ark grey shaded area*: 95% confidence interval of the estimated slope of the *Deming* regression line, d*ashed lines*: medians of x and y axis estimated on the 293 species.
Filled symbols: 204 species included in the models, o*pen symbols:* 89 species not included in the models due to missing data for some predictors. *Blue triangles:* unexpected species but consistent with the predicted positive relationship between juvenile survival and longevity, *red circles:* unexpected species and non-consistent with the predicted positive relationship between juvenile survival and longevity, *black squares*: expected species.

b) Number in parenthesis corresponds to the species included in our analysis, for which we had complete set of information. Grey number represents percentages. Above and below refers to a). Table 3-S5 show how species from each of these categories are characterized by the 20 parameters investigated in this study.

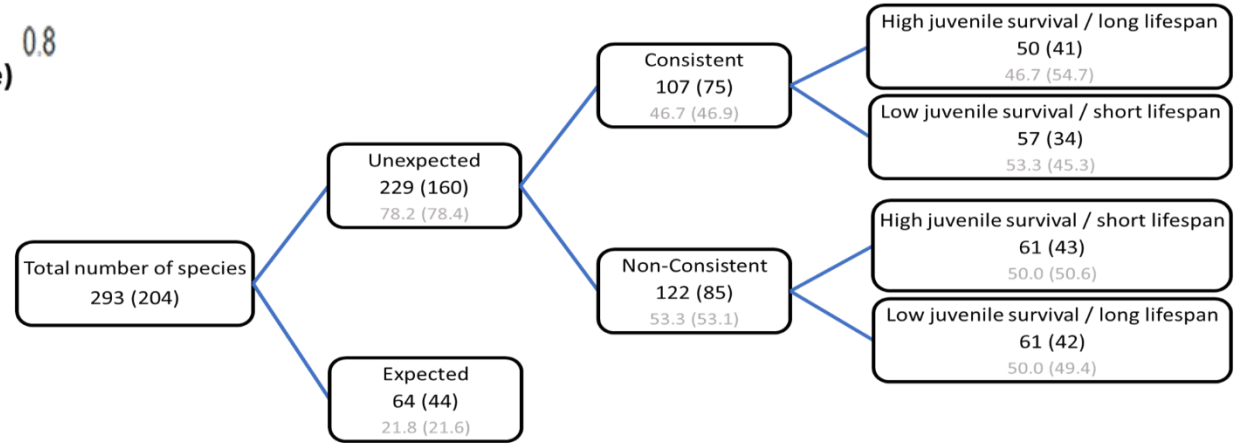


Figure 3-1. (a) Relationship between juvenile survival and longevity used to categorize the species; **(b)** Distribution of the species based on the categorization (see Table 3-3 for details on the categorization).

3.3 Results

3.3.1 CORRELATES OF JUVENILE SURVIVAL AND LONGEVITY

Juvenile survival (first-year survival rate) ranged from 0.08 to 0.95 (0.39 ± 0.16; mean ± SD) and maximum longevity from 5 to 51 (17.7 ± 9.0) years. Both survival estimates were positively correlated with each other (N = 204, slope = 12.5, $r_{Spearman}$= 0.27, $p < 0.005$). Juvenile survival and longevity correlated with life-history pace where species with a slow life-history pace (i.e., a large body size, a long incubation and nestling period, a low reproductive investment, Table 3-2) had significantly higher juvenile survival and greater longevity than species with a fast life-history pace (Table 3-4). Moreover, juvenile survival was higher in species with a high nest predation risk (Table 3-1 and 3-4), while longevity was greater in species with a low exposure to predators of adults (Table 3-4). The phylogenetic effect was only significant for longevity (Table 3-4).

3.3.2 UNEXPECTED AND NON-CONSISTENT COMBINATION OF JUVENILE SURVIVAL AND LONGEVITY

Despite the positive correlation between juvenile survival and longevity, 229 of 293 species fell outside the 95% confidence interval of the regression (i.e., unexpected species; Figure 3-1). Thereof, 107 species still had a positive relationship between juvenile survival and longevity, having either a high juvenile survival associated with a long lifespan (N = 50 species) or a low juvenile survival associated with a short lifespan (N = 57 species). However, 122 species had a non-consistent relationship between juvenile survival and longevity, with 61 species having a low juvenile survival associated with a long lifespan, and 61 species having a high juvenile survival associated with a short lifespan (Figure 3-1).

Table 3-4. Results from phylogenetically controlled linear mixed-effect models testing the influence of key life-history, ecological and social traits on juvenile survival and longevity.

		Juvenile survival (first-year survival rate)			**longevity** (maximum longevity)		
		Fs_{300}	95% CI	estimates*	estimates*	95% CI	Fs_{300}
(intercept)		0.02	(0.19,0.21)	0.20	**-0.70**	(-0.70,-0.70)	**1**
residual adult body mass (covariate)		0	(-0.02,-0.02)	-0.02	0.03	(0.03,0.03)	0
ln (research effort) (covariate)		**1**	(-0.14,-0.14)	**-0.14**	**0.18**	(0.18,0.18)	**1**
life-history pace		**1**	(0.50,0.50)	**0.50**	**0.42**	(0.42,0.42)	**1**
nest predation risk		**0.92**	(0.19,0.19)	**0.19**	-0.10	(-0.10,-0.10)	0
exposure to predators		0	(-0.17,-0.17)	-0.17	**-0.22**	(-0.22,-0.22)	**0.88**
MGS duration		0	(-0.01,-0.01)	-0.01	-0.08	(-0.08,-0.08)	0
N avian predators		0	(0.07,0.07)	0.07	-0.05	(-0.05,-0.05)	0
foraging cost		0	(-0.14,-0.14)	-0.14	-0.06	(-0.06,-0.06)	0
food fiber		0	(-0.13,-0.13)	-0.13	0.03	(0.03,0.04)	0
social system	family-living	0	na	0.00	0.00	na	0
	non family-living		(-0.23,-0.23)	-0.23	-0.25	(-0.25,-0.25)	
period of activity	diurnal	0	na	0.00	0.00	na	0
	nocturnal		(0.31,0.31)	0.31	-0.38	(-0.38,-0.38)	
parental care mode	biparental	0	na	0.00	0.00	na	0
	cooperation		(-0.08,-0.08)	-0.08	-0.17	(-0.17,-0.17)	
	uniparental		(0.52,0.53)	0.53	0.34	(0.34,0.34)	
sedentariness	resident	0	na	0.00	0.00	na	0
	migratory		(0.14,0.14)	0.14	0.07	(0.07,0.07)	
diet specialization	generalist	0	na	0.00	0.00	na	0
	specialist		(0.04,0.04)	0.04	-0.07	(-0.07,-0.07)	
habitat specialization	generalist	0	na	0.00	0.00	na	0
	specialist		(0.10,0.10)	0.10	-0.11	(-0.12,0.11)	
chick development mode	non-precocial	0	na	0.00	0.00	na	0
	precocial		(-0.10,-0.10)	-0.10	-0.36	(-0.36,-0.36)	
region	both	0	na	0.00	0.00	na	0
	island		(-0.32,-0.31)	-0.32	-0.12	(-0.12,-0.12)	
	northern		(0.39,0.39)	0.39	-0.16	(-0.16,-0.16)	
	southern		(0.35,0.35)	0.35	-0.21	(-0.21,-0.21)	

Bold estimates correspond to predictors with significant effect. na – not applicable.
95% CI: confidence interval of the average estimate on the 300 trees
Fs_{300}: frequency of trees for which p-values < 0.05.
*: reference level of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.
Phylogenetic effect longevity model: likelihood ratio test: LRT = 28.69, df = 1, p < 0.005
Phylogenetic effect juvenile survival model: likelihood ratio test: LRT = 3.25, df = 1, p = 0.07

Unexpected species deviated more from the juvenile survival-longevity regression when experiencing a low exposure to predators of adults, having a slow life history pace, being a habitat generalist, nocturnal or when having uniparental brood care (Figure 3-2 and Table 3-S1). Yet, the direction of the deviation had no effect on any of these predictors. In contrast, the direction of deviations was important for non-consistent species, which were influenced by exposure to predators of adults, the duration of the growing season, diet specialization, chick development mode and parental care mode (Figure 3-2 and Table 3-S2). Species with a high juvenile survival associated with a short lifespan occurred in environments with a long duration of the growing season, had a specialized diet, were precocial, or breed cooperatively. In contrast, species with a low juvenile survival associated with a long lifespan had a short duration of the growing season, a low exposure to predators of adults, or uniparental brood care (Figure 3-3a – e and Table 3-S2). The degree of deviation of the non-consistent species was also associated with a nocturnal lifestyle but this effect was independent of the direction of the deviation.

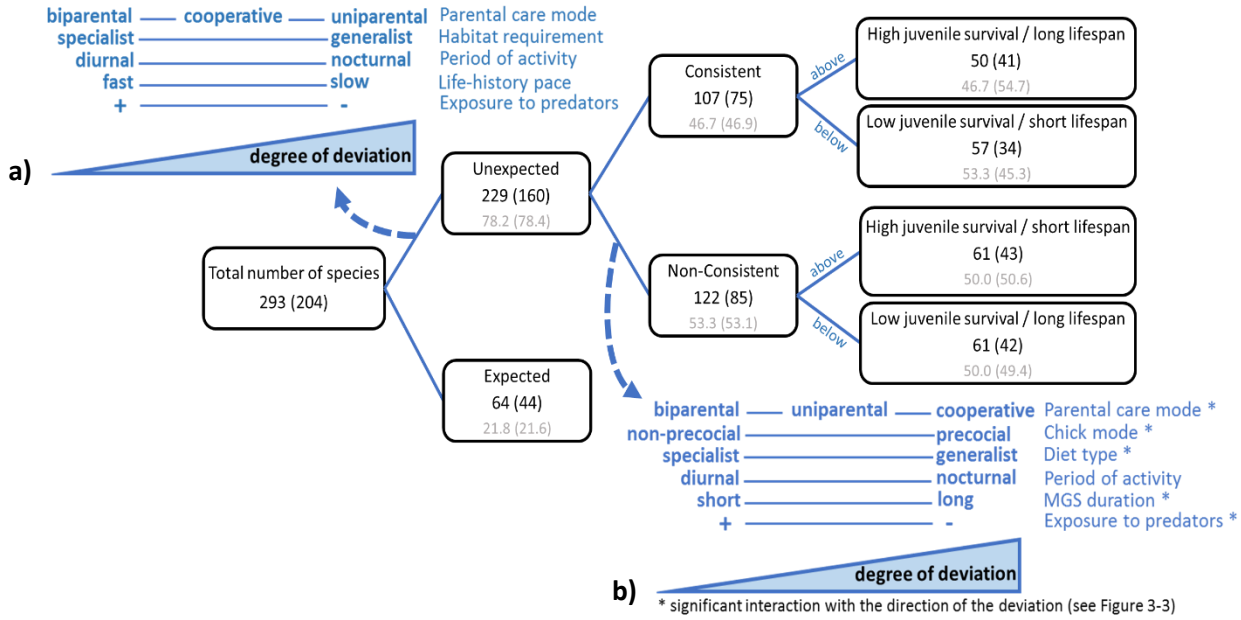


Figure 3-2. Graphical summary of the results from backward model selection on phylogenetically controlled linear mixed-effect model investigating which life-history, ecological and social traits characterize species with **(a)** unexpected and **(b)** unexpected-non-consistent longevity vs. juvenile survival relationship. (Estimates presented in Table 3-S1 for **(a)** and in Table 3-S2 for **(b)**).

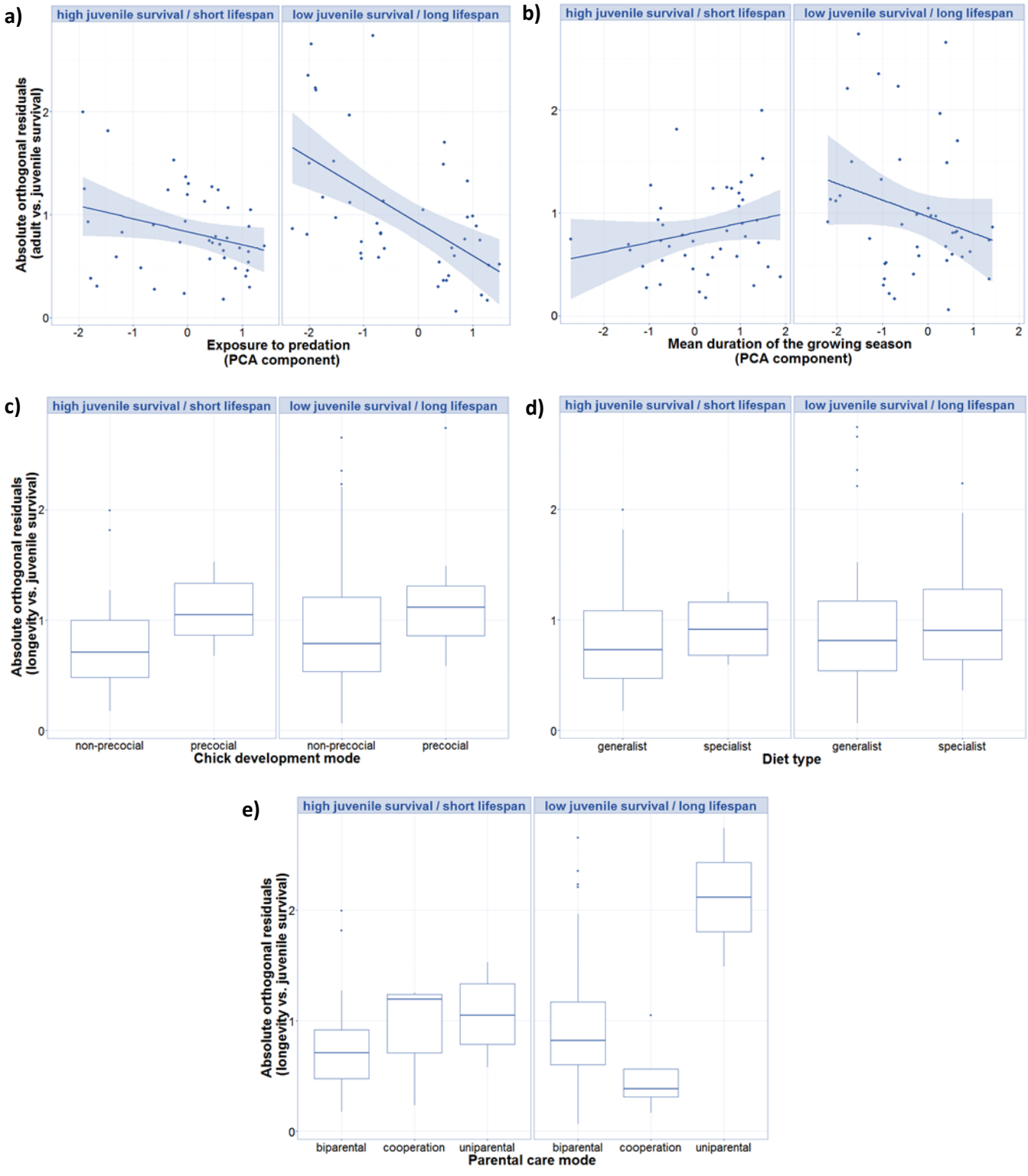


Figure 3-3. Absolute orthogonal residuals of the relationship between longevity and juvenile survival (degree of deviation) for non-consistent species with unusually low juvenile survival and long lifespan vs. unusually high juvenile and short lifespan (respectively above vs. below the *Deming* regression line, Figure 3-1). Degree of deviation in function of **(a)** exposure to predation (Table 3-1 and 3-2), **(b)** mean duration of the growing season, **(c)** chick development mode, **(d)** diet type and **(e)** parental care mode.

3.4 Discussion

Life-history studies often use longevity as a surrogate of life-history pace based on the assumption that juvenile survival and longevity are positively correlated (Williams 1957; Charlesworth 1994; Keller & Genoud 1997; Ricklefs & Scheuerlein 2003). Yet, our results show that almost 80% of bird species deviate significantly from the overall regression over juvenile survival and longevity. This finding highlights the importance to consider age-specific mortality (Schaffer 1974; Michod 1979; Reznick, Bryga & Endler 1990; Promislow & Harvey 1991; Martin 2002; Kraus *et al.* 2005; Martin 2014) and the relationship between juvenile survival and longevity. Our analyses confirm that on average a slow life-history pace is associated with high juvenile survival and long lifespan and show that distinct external predation risks correlated with each survival estimates (Table 3-4). Yet, we find that ecological (exposure to predators, length of growing season, feeding habits, period of activity), life-history (chick development mode) and social traits (parental care mode) are associated with deviation from the general trend of a positive relationship between juvenile and adult survival (Figure 3-2, Table 3-S1 and 3-S2).

The association of high juvenile survival and long lifespan with a slow pace of life supports the general life-history theory (Stearns 1992; Charlesworth 1994). However, while juvenile and adult survival in birds were positively correlated, their variation was also associated with particular parameters (Francis *et al.* 1992), which is in accordance with findings from mammals (Promislow & Harvey 1990). A high exposure to predators (Table 3-1 and 3-2) was only associated with low adult survival but not juvenile survival (Table 3-4). A possible explanation is that in contrast to adults, juveniles have often more cryptic coloration and behaviors than adults (Heinen 1985; Ryer *et al.* 2008; Jenni & Winkler 2011), making them generally less conspicuous to predators. When controlling for life-history and adult body mass we found that a low juvenile survival, but not adult survival, was associated with a low nest predation risk (Table 3-4 and Table 3-1 for details on nest predation risk parameter). It either suggests that nest modus and breeding location are mainly

detrimental to juveniles while, in average, it does not affect adult survival or, that juvenile over adult survival has a higher selective role on nest modus and nest site location in birds. Why low nest predation risk correlated with low juvenile survival? Based on our categorization for nest predation risk a low risk is equivalent to cavity nesting mode (Table 3-1). While cavity breeding species often experience lower nest predation risk than open-nesting species (Martin & Li 1992), their nestlings are frequently exposed to ectoparasites (Nilsson 1986; Cantarero *et al.* 2013), reducing their body condition (Tomas *et al.* 2008; Brommer *et al.* 2011; Cantarero *et al.* 2013) and therefore, potentially reducing post-fledging survival (this study; Francis *et al.* 1992). Alternatively, open-nesting species experience high nest predation rates and consequently, offspring that successfully fledge may be of generally high quality. This finding suggests that nesting habits might have long-term consequences that so far were not anticipated (but see Martin 2014).

Most species (78%) deviated significantly from the positive juvenile survival-longevity regression (unexpected species; Figure 3-1). Our approach does not allow to investigate from those deviations unusual juvenile survival and longevity separately. Therefore, underlying mechanism cannot be identified. Nevertheless, we can assume that deviations may reflect age-dependent changes in body size, coloration, behavior, or life-history (i.e., onset of reproduction, senescence), exposing individuals to different selection pressures that affect both extrinsic and intrinsic mortality differently at different life stages (Lack 1966; Sullivan 1989). Similar proportion of species showed concordant (consistent species) and contrasting combination of juvenile survival and longevity (non-consistent species) (Figure 3-1). Those divergent patterns might be explained by the existence on one hand, of factors that loosen the relationship between juvenile survival and longevity by acting in opposite direction and favor the evolution of independent values and, on the other hand, of factors that enforce strong bonds in the same direction. Interestingly, passerines were mostly among unexpected species (Table 3-S3). Orders with mostly non-consistent species were non-passerines (*Accipitriformes, Columbiformes, Galliformes, Pelecaniformes* and *Strigiformes*; considering taxonomic orders with more than five species and

for which more than 60% were classified as “non-consistent”, Table 3-S3 and 3-S4). Most *Accipitriformes, Anseriformes, Charadriiformes and Pelicaniformes* with non-consistent deviation showed a low juvenile survival but long lifespan, while principally a high juvenile survival but short lifespan was found in non-consistent *Columbiformes* and *Passeriformes* (using the same criteria as above, Table 3-S3 and 3-S4). We discuss below first the factors that are associated with unexpected species and thereafter those that specifically associated with non-consistent species.

3.4.1 UNEXPECTED SPECIES

Deviations from the positive relationship between juvenile survival and longevity are associated with life-history, ecological and social factors. Species with a slow pace of life, nocturnal, habitat generalist, with a low exposure to predators, or uniparental breeding had larger deviation (Figure 3-2 and Table 3-S1). The expression of such traits could be favored by unexpected survival ratio. Alternatively, they might increase or release selective pressure on survival differently depending on the stage of life and impose less pressure to maintain strong relationship between juvenile survival and longevity. For instance, we show that juvenile survival and longevity are less related in species with slow pace of life. A possible explanation for this pattern could be that, because slow life-history pace imposes less selection on many physiological components and other attributes of individuals’ life (Flatt & Heyland 2011) (i.e., less constraining in term of selection pressure), it gives leave to the expression of independent juvenile and adult survival.

Interestingly, the association of the abovementioned life-history, ecological and social factors with the degree of deviation was not affected by the direction of this deviation (Figure 3-2 and Table 3-S1). Hence, similar evolutionary pressures might relate to the expression of longer lifespan and lower juvenile survival or shorter lifespan and higher juvenile survival than expected under the general pattern of a positive relationship between juvenile survival and longevity (i.e., deviations above and below the juvenile survival / longevity function; Figure 3-1).

3.4.2 NON-CONSISTENT SPECIES

The direction of deviation influences how the degree in which non-consistent species deviate responds to the duration of the growing season, diet, chick development mode, or parental care mode, except the period of activity (Figure 3-2 and Table 3-S2). Thus, evolution of low juvenile survival / long lifespan vs. high juvenile survival / short lifespan might have happened under opposite life-history, ecological and social conditions. Alternatively, opposite life-history, ecological and social factors favored or constrained the evolution of inverted contrasting juvenile survival-longevity combination (i.e. low/short vs. high/long).

Our results show that combination of high juvenile survival but short lifespan is associated with a long duration of the growing season, a specialized diet, precociality, or cooperative breeding, while a low juvenile survival but a long lifespan associated with a low exposure to predators, uniparental care, or short duration of the growing season (Figure 3-2 and Table 3-S2). Environments with a long growing season (i.e., sub-tropics and tropics) might be particularly beneficial for juvenile survival due to continuous abundance of resources and the absence of harsh periods (McNamara *et al.* 2008; Tarwater *et al.* 2011). Alternatively, these environments allow for a prolonged investment of parents into their offspring, and family living occurs especially in environments with a long growing season (Valcu *et al.* 2014). The long lifespan in environments with a short growing season might reflect a lower abundance of predators of adults (Valcu *et al.* 2014) however, we did not find any influence of the number of avian predators on longevity (Table 3-4). Young in cooperatively breeding species are feed by more than two adults, and spend a prolonged time after independency with their parents, which might both boost juvenile survival. In contrast, the long lifespan in species with uniparental brood care may rather reflect a low juvenile survival, given that these species overall might provide less care for offspring than species with bi-parental brood care (Royle, Smiseth & Kölliker 2012).

Interestingly, duration of the growing season, diet and chick development mode only related to negative juvenile survival-longevity relationship. In contrast, as life-history pace was only significant when all type of deviations were considered but not when we only investigated the non-consistent deviations, one can assumes that the pace of life accounted principally for unexpected positive relationship between juvenile survival and longevity estimates. This partly supports the findings from McNacamara et al. (2008) that higher first-year survival in parallel with higher adult survival is predicted in species with slow life histories.

To conclude, our comparative study provides novel insights into interspecific variation in age-specific survival. Associations between juvenile survival and longevity that deviate from the general pattern of a positive correlation are found in many species and different ecological, life-history and social factors are associated with the different types of deviations (for simple description see Table 3-S5). Distinct environmental factors linked with predation risk associated with juvenile survival and longevity, however, they related in both cases with life-history pace. We highlight that life-history factors that provide short-term benefits (i.e., a lower nest predation risk), can have negative down-stream effect on juvenile survival (i.e., low juvenile survival). Overall, our results insinuate that interspecific diversity in juvenile survival and longevity relationship results from divergent patterns of selection. Alternatively, they suggest that divergent age-specific survival is at the origin of diversity in species attributes which supports the importance to consider age-specific survival to understand the evolution of life-history traits. Finally, as species with unusual age-specific survival relationships are more likely to evolve unusual combination of life-history traits, our study, by identifying key factors associating with unusual age-specific survival, could contribute to a better understanding of life-history evolution.

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Appendix Chapter 3

Table 3-S1. Results from backward model selection on phylogenetically controlled linear mixed-effect model investigating which life-history, ecological and social traits characterize species with unexpected juvenile survival-longevity relationship (160 species).

predictors		estimates*	95% CI	Fs_{300}
(intercept)		0.97	(0.97,0.97)	**1**
residual adult body mass (covariate)		-0.01	(-0.01,-0.01)	0
ln (research effort) (covariate)		-0.03	(-0.03,-0.03)	0
exposure to predators		-0.24	(-0.24,-0.24)	**1**
life-history pace		0.19	(0.19,0.19)	**1**
period of activity	diurnal	0.00	na	**1**
	nocturnal	0.35	(0.35,0.35)	
habitat requirement	generalist	0.00	na	**1**
	specialist	-0.25	(-0.25,-0.25)	
parental care mode	biparental	0.00	na	**1**
	cooperation	0.17	(0.17,0.17)	
	uniparental	0.37	(0.37,0.37)	

Note: all interaction with the sign of the residuals were non-significant. na – not applicable.
Predictors with significant effect on the response variable are in **bold**.
*: reference level of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.
95% CI: confidence interval of the average estimate on the 300 trees.
Fs_{300}: frequency of trees for which p-values < 0.05.
Phylogenetic effect: likelihood ratio test: p = 1.

Table 3-S2. Results from backward model selection on phylogenetically controlled linear mixed-effect model investigating which life-history, ecological and social traits characterize species with unexpected and non-consistent juvenile survival-longevity relationship (85 species).

predictors		estimates*	95% CI	Fs_{300}
simples effects:				
(intercept)		0.62	(0.62,0.62)	**1**
residual adult body mass (covariate)		-0.03	(-0.03,-0.03)	0
ln (research effort) (covariate)		0.01	(0.01,0.01)	0
exposure to predators		-0.13	(-0.13,-0.13)	**1**
MGS duration		0.04	(0.04,0.04)	**1**
residuals sign	-	0.00	na	0
	+	-0.04	(-0.04,-0.04)	
period of activity	diurnal	0.00	na	**1**
	nocturnal	0.52	(0.52,0.52)	
diet type	generalist	0.00	na	**1**
	specialist	-0.08	(-0.08,-0.08)	
chick development mode	non-precocial	0.00	na	**1**
	precocial	0.26	(0.26,0.26)	
parental care mode	biparental	0.00	na	**1**
	cooperation	0.27	(0.27,0.27)	
	uniparental	0.21	(0.21,0.21)	
interactions:				
residuals sign : exposure to predators	-	0.00	na	**1**
	+	-0.26	(-0.26,-0.26)	
residuals sign : MGS duration	-	0.00	na	**1**
	+	-0.31	(-0.31,-0.31)	
residuals sign : diet type	- : generalist	0.00	na	**1**
	- : specialist	0.00	na	
	+ : generalist	0.00	na	
	+ : specialist	0.59	(0.59,0.59)	
residuals sign : chick development mode	- : non-precocial	0.00	na	**1**
	- : precocial	0.00	na	
	+ : non-precocial	0.00	na	
	+ : precocial	-1.02	(-1.02,-1.02)	
residuals sign : parental care mode	- : biparental	0.00	na	**1**
	- : cooperation	0.00	na	
	- : uniparental	0.00	na	
	+ : biparental	0.00	na	
	+ : cooperation	-0.28	(-0.28,-0.28)	
	+ : uniparental	1.83	(1.83,1.83)	

Predictors with significant effect on the response variable are in **bold**. na – not applicable.

*: reference level of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

95% CI: confidence interval of the average estimate on the 300 trees.

Fs_{300}: frequency of trees for which p-values < 0.05.

Phylogenetic effect: likelihood ratio test: p = 1.

Table 3-S3. Species distribution by taxonomic order and based on the characteristics of their combination of juvenile survival-longevity.

order	total	expected	unexpected (all)	unexpected					
				consistent			non-consistent		
				all	below	above	all	below	above
Accipitriformes	19	4 (21)	15 (79)	5 (33)	2 (40)	3 (60)	10 (67)	1 (10)	9 (90)
Anseriformes	24	9 (38)	15 (62)	8 (53)	5 (62)	3 (38)	7 (47)	1 (14)	6 (86)
Apodiformes	4	0 (0)	4 (100)	4 (100)	4 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Charadriiformes	52	9 (17)	43 (83)	23 (54)	11 (48)	12 (52)	20 (46)	7 (35)	13 (65)
Ciconiiformes	2	1 (50)	1 (50)	1 (100)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Columbiformes	8	0 (0)	8 (100)	2 (25)	2 (100)	0 (0)	6 (75)	4 (67)	2 (33)
Coraciiformes	3	0 (0)	3 (100)	0 (0)	0 (0)	0 (0)	3 (100)	2 (67)	1 (33)
Falconiformes	8	1 (12)	7 (88)	3 (43)	2 (67)	1 (33)	4 (57)	2 (50)	2 (50)
Galliformes	8	2 (25)	6 (75)	1 (17)	1 (100)	0 (0)	5 (83)	4 (80)	1 (20)
Gruiformes	4	3 (75)	1 (25)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	1 (100)
Passeriformes	121	28 (23)	93 (77)	52 (56)	27 (52)	25 (48)	41 (44)	30 (73)	11 (27)
Pelecaniformes	11	1 (9)	10 (91)	1 (10)	0 (0)	1 (100)	9 (90)	0 (0)	9 (100)
Phaethontiformes	1	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Piciformes	1	0 (0)	1 (100)	1 (100)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Podicipediformes	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Procellariiformes	5	0 (0)	5 (100)	1 (20)	0 (0)	1 (100)	4 (80)	1 (25)	3 (75)
Psittaciformes	2	0 (0)	2 (100)	0 (0)	0 (0)	0 (0)	2 (100)	2 (100)	0 (0)
Sphenisciformes	2	1 (50)	1 (50)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Strigiformes	9	3 (33)	6 (67)	2 (33)	0 (0)	2 (100)	4 (67)	3 (75)	1 (25)
Suliformes	8	1 (12)	7 (88)	3 (43)	1 (33)	3 (67)	4 (57)	2 (50)	2 (50)
Grand Total	293	64 (22)	229 (78)	107 (47)	57 (53)	50 (47)	122 (53)	61 (50)	61 (50)

Number in parenthesis represents percentages. Expected, non-expected, consistent, non-consistent, above, below refers to Figure 3-1.

Table 3-S4. Species distribution by taxonomic family and based on the characteristics of their combination of juvenile survival-longevity (following on the next page).

family	total	expected	unexpected (all)	unexpected					
				consistent			non-consistent		
				all	below	above	all	below	above
Acanthisittidae	1	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Acanthizidae	3	2 (67)	1 (33)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	1 (100)
Accipitridae	18	3 (17)	15 (83)	5 (33)	2 (40)	3 (60)	10 (67)	1 (10)	9 (90)
Aegithalidae	1	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Alaudidae	1	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Alcedinidae	2	0 (0)	2 (100)	0 (0)	0 (0)	0 (0)	2 (100)	1 (50)	1 (50)
Alcidae	8	0 (0)	8 (100)	1 (12)	1 (100)	0 (0)	7 (88)	2 (29)	5 (71)
Anatidae	24	9 (37)	15 (63)	8 (53)	5 (62)	3 (38)	7 (47)	1 (14)	6 (86)
Anhingidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Apodidae	3	0 (0)	3 (100)	3 (100)	3 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Ardeidae	7	1 (14)	6 (86)	0 (0)	0 (0)	0 (0)	6 (100)	0 (0)	6 (100)
Burhinidae	1	0 (0)	1 (100)	1 (100)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Cathartidae	1	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Charadriidae	8	2 (25)	6 (75)	3 (50)	2 (67)	1 (33)	3 (50)	2 (67)	1 (33)
Ciconiidae	2	1 (50)	1 (50)	1 (100)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Cinclidae	2	0 (0)	2 (100)	1 (50)	1 (100)	0 (0)	1 (50)	1 (100)	0 (0)
Climacteridae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Colluricinclidae	1	0 (0)	1 (100)	1 (100)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Columbidae	8	0 (0)	8 (100)	2 (25)	2 (100)	0 (0)	6 (75)	4 (67)	2 (33)
Corvidae	17	4 (24)	13 (76)	8 (62)	7 (87)	1 (13)	5 (38)	1 (20)	4 (80)
Dicaeidae	1	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Diomedeidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	1 (100)
Emberizidae	7	2 (29)	5 (71)	3 (60)	0 (0)	3 (100)	2 (40)	2 (100)	0 (0)
Estrildidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Falconidae	8	1 (12)	7 (88)	3 (43)	2 (67)	1 (33)	4 (57)	2 (50)	2 (50)
Fringillidae	11	2 (18)	9 (82)	4 (44)	2 (50)	2 (50)	5 (56)	4 (80)	1 (20)
Gruidae	2	2 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Hirundinidae	9	2 (22)	7 (78)	4 (57)	1 (25)	3 (75)	3 (43)	3 (100)	0 (0)
Icteridae	2	0 (0)	2 (100)	1 (50)	1 (100)	0 (0)	1 (50)	1 (100)	0 (0)
Laridae	17	3 (18)	14 (82)	10 (71)	4 (40)	6 (60)	4 (29)	0 (0)	4 (100)
Maluridae	3	1 (33)	2 (67)	2 (100)	2 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Meliphagidae	5	1 (20)	4 (80)	4 (100)	0 (0)	4 (0)	0 (0)	0 (0)	0 (0)
Momotidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Motacillidae	4	1 (25)	3 (75)	1 (33)	1 (100)	0 (0)	2 (67)	2 (100)	0 (0)
Muscicapidae	5	2 (40)	3 (60)	2 (67)	1 (50)	1 (50)	1 (33)	1 (100)	0 (0)
Odontophoridae	1	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Paridae	5	0 (0)	5 (100)	3 (60)	0 (0)	3 (100)	2 (40)	2 (100)	0 (0)
Parulidae	5	1 (20)	4 (80)	2 (50)	1 (50)	1 (50)	2 (50)	2 (100)	0 (0)

Number in parenthesis represents percentages. Expected, non-expected, consistent, non-consistent, above, below refers to Figure 3-1.

Table 3-S4 following. Species distribution by taxonomic family and based on the characteristics of their combination of juvenile survival-longevity.

family	total	expected	unexpected (all)	unexpected					
				consistent			non-consistent		
				all	below	above	all	below	above
Passeridae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	1 (100)
Pelecanidae	2	0 (0)	2 (100)	1 (50)	0 (0)	1 (100)	1 (50)	0 (0)	1 (100)
Petroicidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Phaethontidae	1	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Phalacrocoracidae	5	1 (20)	4 (80)	3 (75)	1 (33)	2 (67)	1 (25)	1 (100)	0 (0)
Phasianidae	7	1 (14)	6 (86)	1 (17)	1 (100)	0 (0)	5 (83)	4 (80)	1 (20)
Picidae	1	0 (0)	1 (100)	1 (100)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Pipridae	1	0 (0)	1 (100)	1 (100)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)
Ploceidae	3	0 (0)	3 (100)	1 (33)	0 (0)	1 (100)	2 (67)	2 (100)	0 (0)
Podicipedidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Polioptilidae	1	0 (0)	1 (100)	1 (100)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Pomatostomidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Procellariidae	4	0 (0)	4 (100)	1 (25)	0 (0)	1 (100)	3 (75)	1 (33)	2 (67)
Prunellidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	1 (100)
Psittacidae	2	0 (0)	2 (100)	0 (0)	0 (0)	0 (0)	2 (100)	2 (100)	0 (0)
Ptilonorhynchidae	1	0 (0)	1 (100)	1 (100)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)
Pycnonotidae	1	0 (0)	1 (100)	1 (100)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)
Rallidae	2	1 (50)	1 (50)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	1 (100)
Recurvirostridae	3	1 (33)	2 (67)	0 (0)	0 (0)	0 (0)	2 (100)	2 (100)	0 (0)
Remizidae	1	0 (0)	1 (100)	1 (100)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Scolopacidae	13	1 (8)	12 (92)	8 (67)	3 (37)	5 (63)	4 (33)	1 (25)	3 (75)
Sittidae	2	1 (50)	1 (50)	1 (100)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Spheniscidae	2	1 (50)	1 (50)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Stercorariidae	2	2 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Strigidae	8	3 (37)	5 (63)	2 (40)	0 (0)	2 (100)	3 (60)	3 (100)	0 (0)
Sturnidae	2	0 (0)	2 (100)	0 (0)	0 (0)	0 (0)	2 (100)	1 (50)	1 (50)
Sulidae	2	0 (0)	2 (100)	0 (0)	0 (0)	0 (0)	2 (100)	0 (0)	2 (100)
Sylviidae	10	3 (30)	7 (70)	6 (86)	3 (50)	3 (50)	1 (14)	1 (100)	0 (0)
Threskiornithidae	2	0 (0)	2 (100)	0 (0)	0 (0)	0 (0)	2 (100)	0 (0)	2 (100)
Timaliidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Trochilidae	1	0 (0)	1 (100)	1 (100)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)
Troglodytidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Turdidae	6	1 (17)	5 (83)	3 (60)	3 (100)	0 (0)	2 (40)	0 (0)	2 (100)
Tytonidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	1 (100)
Vireonidae	1	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Zosteropidae	1	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	0 (0)
Grand Total	293	64 (22)	229 (78)	107 (47)	57 (53)	50 (47)	122 (53)	61 (50)	61 (50)

Number in parenthesis represents percentages. Expected, non-expected, consistent, non-consistent, above, below refers to Figure 3-1.

Table 3-S5. Characterization of the 160 unexpected species over 204 species for which we had data on each predictors investigated in this study in function of the nature of their relationship between juvenile survival and longevity.

			consistent			non-consistent		
	variables		all	below	above	all	below	above
			n = 75	n = 41	n = 34	n = 85	n = 43	n = 42
effectives	region	both	10	3	7	9	1	8
		island	2	1	1	3	0	3
		northern	52	31	21	61	31	30
		southern	11	6	5	12	10	2
	chick development mode	non-precocial	64	33	31	71	35	36
		precocial	11	8	3	14	7	7
	habitat requirement	generalist	36	69	20	40	20	20
		specialist	39	25	14	45	22	23
	diet type	generalist	60	30	30	61	32	29
		specialist	15	11	4	24	10	14
	sedentariness	resident	26	16	10	28	17	11
		migratory	49	25	24	57	25	32
	parental care mode	biparental	65	33	32	67	30	37
		cooperation	6	5	1	9	5	4
		uniparental	4	3	1	9	7	2
	period of activity	diurnal	71	40	31	76	37	39
		nocturnal	4	1	3	9	5	4
	social system	non family living	54	28	26	61	30	31
		family-living	21	13	8	24	12	12
means ± SD	residual adult body mass (covariate)		-0.13 ±0.84	-0.07 ±0.87	-0.20 ±0.82	0.06 ±0.77	-0.12 ±0.78	0.23 ±0.73
	ln (research effort) (covariate)		5.35 ±1.31	5.07 ±1.08	5.70 ±1.49	5.72 ±1.38	5.15 ±1.27	6.27 ±1.28
	lie-history pace*		-0.05 ±0.95	0.02 ±0.97	-0.14 ±0.92	0.17 ±0.89	-0.08 ±0.92	0.42 ±0.78
	exposure to predators *		0.09 ±0.98	0.15 ±0.89	0.02 ±1.08	-0.13 ±1.09	0.05 ±0.99	-0.30 ±1.17
	food fiber *		0.02 ±1.00	-0.01 ±1.14	0.06 ±0.82	-0.01 ±0.99	-0.23 ±0.97	0.20 ±0.98
	nest predation risk *		0.08 ±0.99	0.22 ±0.99	-0.08 ±0.97	-0.16 ±1.00	-0.15 ±1.06	-0.18 ±0.96
	foraging cost *		0.09 ±0.87	0.15 ±0.84	0.01 ±0.91	0.06 ±1.05	0.10 ±1.09	0.01 ±1.01
	MGS duration *		0.06 ±1.03	0.12 ±0.97	-0.01 ±1.10	-0.05 ±1.05	0.20 ±1.04	-0.30 ±1.00
	N avian predators *		-0.07 ±1.02	-0.02 ±1.13	-0.12 ±0.90	0.12 ±0.98	0.09 ±0.96	0.15 ±1.01

n = sample size; * = predictors representing principal component (Table 3-2)

consistent above, consistent below, non-consistent above and non-consistent below refer to Figure 3-1.

Figure 3-S1. Phylogenetic tree for the set of 293 species (based on the full tree from Jetz *et al.* 2012).

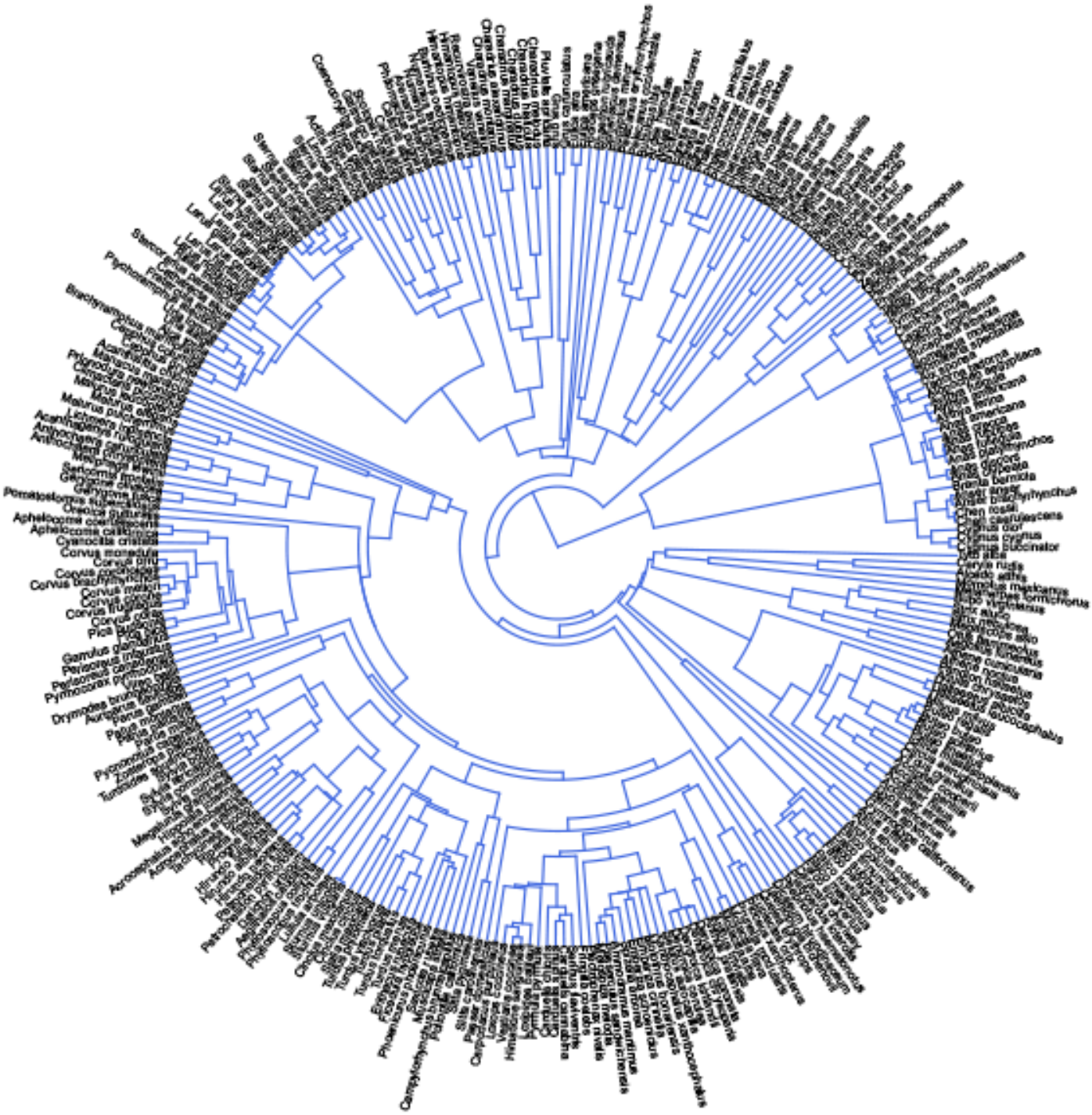


Figure 3-S2. Phylogenetic tree for the set of 204 species representing 18 taxonomic orders and 57 families (based on the full tree from Jetz *et al.* 2012).

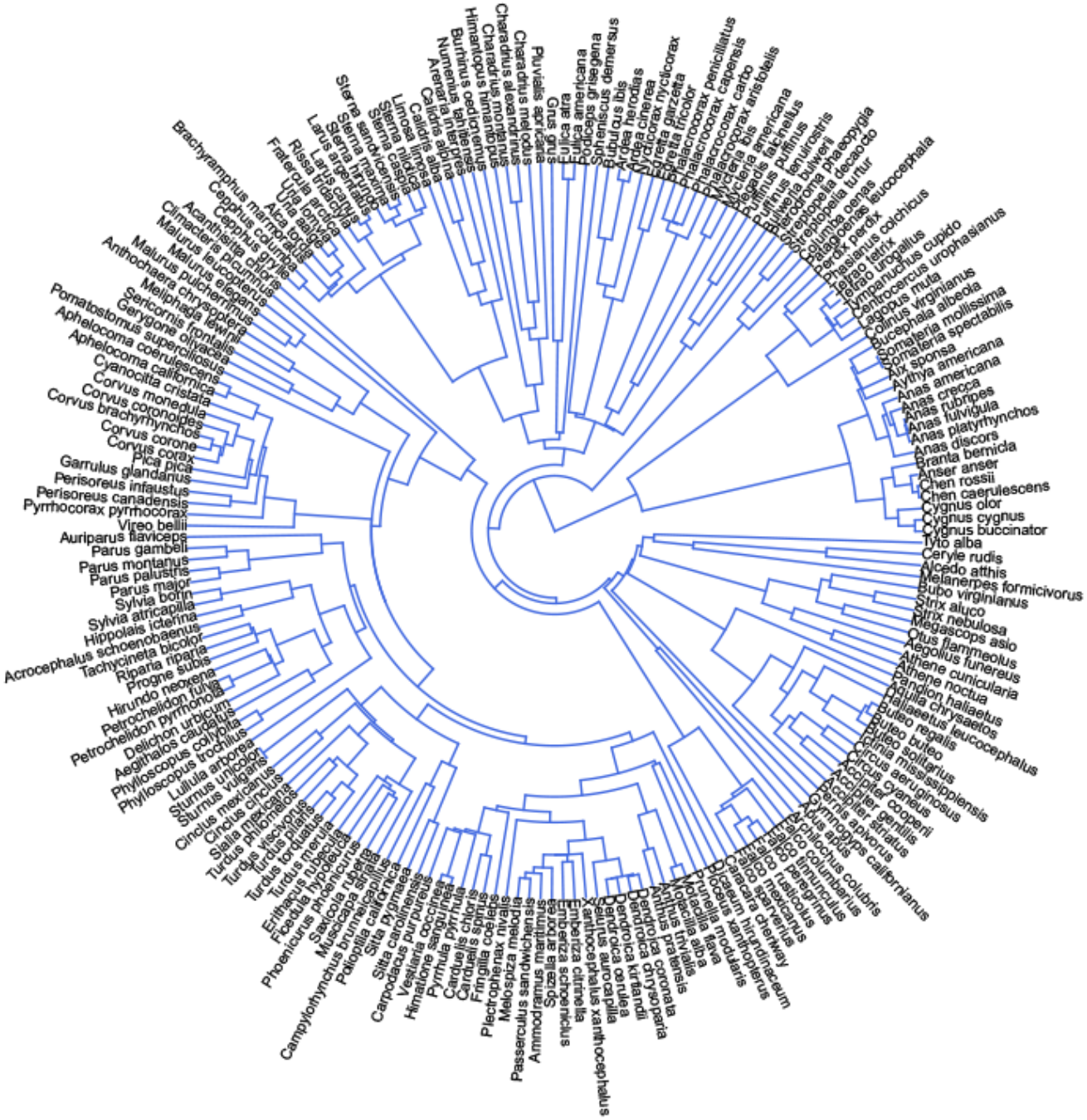
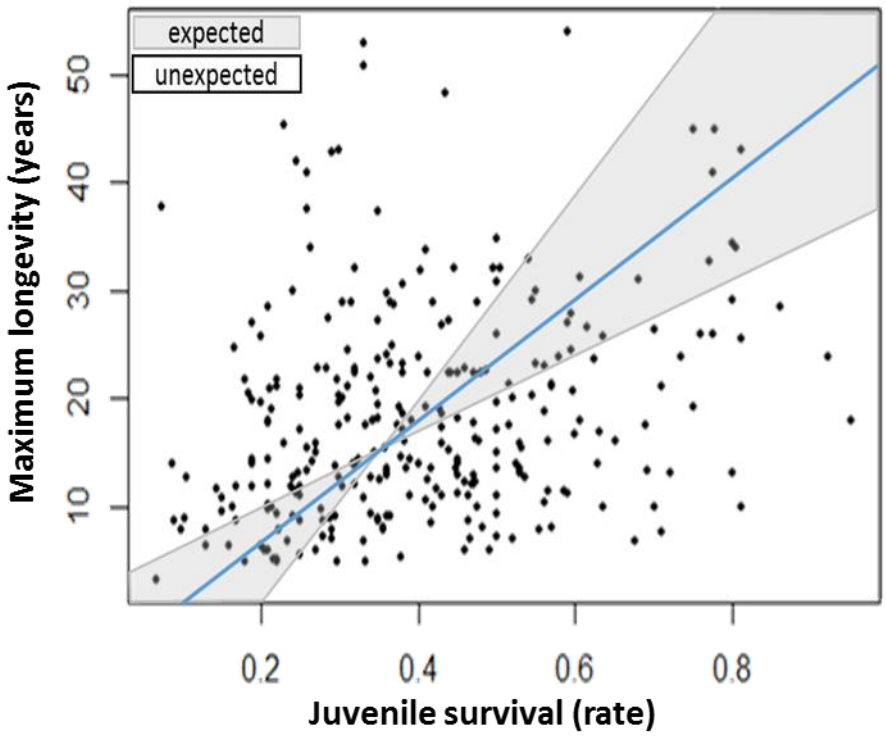

Charadrius melodus
Charadrius alexandrinus
Charadrius montanus
Haematopus palliatus
Haematopus bachmani
Haematopus ostralegus
Haematopus unicolor
Burhinus oedicnemus
Numenius tahitiensis
Arenaria interpres
Calidris alba
Calidris alpina
Limosa limosa
Sterna caspia
Sterna nilotica
Sterna sandvicensis
Sterna maxima
Sterna hirundo
Larus argentatus
Larus canus
Larus fuscus
Rissa tridactyla
Fratercula arctica
Uria aalge
Uria lomvia
Alca torda
Cepphus columba
Cepphus grylle
Brachyramphus marmoratus
Acanthisitta chloris
Climacteris picumnus
Malurus elegans
Malurus leucopterus
Malurus pulcherrimus
Anthochaera chrysoptera
Meliphaga lewinii
Sericornis frontalis
Gerygone olivacea
Pomatostomus superciliosus
Aphelocoma coerulescens
Aphelocoma californica
Cyanocitta cristata
Corvus monedula
Corvus coronoides
Corvus brachyrhynchos
Corvus corone
Corvus corax
Pica pica
Garrulus glandarius
Perisoreus infaustus
Perisoreus canadensis
Pyrrhocorax pyrrhocorax
Vireo bellii
Auriparus flaviceps
Parus gambeli
Parus montanus
Parus palustris
Parus major
Sylvia borin
Sylvia atricapilla
Hippolais icterina
Acrocephalus schoenobaenus
Tachycineta bicolor
Riparia riparia
Progne subis
Hirundo neoxena
Petrochelidon fulva
Petrochelidon pyrrhonota
Delichon urbicum
Aegithalos caudatus
Phylloscopus collybita
Phylloscopus trochilus
Lullula arborea
Sturnus vulgaris
Sturnus unicolor
Cinclus mexicanus
Cinclus cinclus
Sialia mexicana
Sialia philomelos
Turdus viscivorus
Turdus pilaris
Turdus torquatus
Turdus merula
Erithacus rubecula
Ficedula hypoleuca
Phoenicurus phoenicurus
Saxicola rubetra
Muscicapa striata
Campylorhynchus brunneicapillus
Polioptila caerulea
Sitta carolinensis
Sitta pygmaea
Carpodacus purpureus
Vestiaria coccinea
Himatione sanguinea
Pyrrhula pyrrhula
Carduelis chloris
Carduelis spinus
Fringilla coelebs
Plectrophenax nivalis
Melospiza melodia
Passerculus sandwichensis
Ammodramus maritimus
Spizella arborea
Emberiza schoeniclus
Emberiza citrinella
Xanthocephalus xanthocephalus
Seiurus aurocapilla
Dendroica caerulea
Dendroica kirtlandii
Dendroica chrysoparia
Anthus pratensis
Anthus trivialis
Motacilla alba
Motacilla flava
Bombycilla garrulus
Bombycilla cedrorum
Toxostoma rufum
Mimus polyglottos
Sturnus vulgaris
Agelaius phoeniceus
Sturnella magna
Quiscalus quiscula
Molothrus ater
Icterus galbula
Icterus bullockii
Icterus spurius
Icterus wagleri
Icterus pustulatus
Icterus gularis
Icterus graduacauda
Icterus icterus
Cacicus cela
Cacicus haemorrhous
Psarocolius montezuma
Psarocolius decumanus
Psarocolius wagleri
Psarocolius angustifrons
Psarocolius bifasciatus
Psarocolius oseryi
Psarocolius viridis
Psarocolius yuracares
Psarocolius atrovirens
Psarocolius cassini
Psarocolius cassinii
Psarocolius latirostris

Figure 3-S3. *Deming* regression of longevity on juvenile survival (a point represents a species, N = 293).



Regression used to determinate orthogonal residuals between maximum longevity and juvenile survival (first-year survival) and to identify expected (inside the shaded area, N = 64) versus unexpected (outside the shaded area, N = 229) species.
Blue line: Slope of the *Deming* regression (slope = 1.01)
Shaded area: Confidence interval of the estimated slope 95% CI = (0.64, 1.70).

- Chapter 4 -

- Chapter 4 -

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Experience buffers extrinsic mortality in a group-living bird species

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Abstract

Extrinsic mortality has a strong impact on the evolution of life-histories, prey morphology and behavioural adaptations, but for many animals the causes of mortality are poorly understood. Predation is an important driver of extrinsic mortality and mobile animals form groups in response to increased predation risk. Furthermore, in many species juveniles suffer higher mortality than older individuals, which may reflect a lower phenotypic quality, lower competitiveness, or a lack of antipredator or foraging skills. Here we assessed the causes of mortality for 371 radio tagged Siberian jays. This sedentary bird species lives in family groups that contain a breeding pair as well as related and unrelated non-breeders. Ninety-five percent of death were due to predation (N=59 out of 62 individuals) and most individuals were killed by *Accipiter* hawks. Multivariate Cox proportional hazards models showed that non-breeders had a lower survival than breeders, but only in territories in managed forests with little visual cover. Examining breeders, only sex influenced survival with males having a lower survival than females. For non-breeders, juveniles had lower survival than older non-breeders, and those on managed territories had lower survival than those on unmanaged territories. Additionally, a low feather quality reduced the survival probability of non-breeders only. Thus, living on managed territories and having a low feature quality affected only non-breeders, particularly juveniles. These findings add to previous research demonstrating that juvenile Siberian jays acquire critical antipredator skills from experienced group members. Thus, experience can buffer extrinsic mortality, highlighting that group living not only provides safety in numbers, but also provides social opportunities to learn critical life-skills.

Key Words: survival, group-living, sociality, predation, group size, safety in numbers

4.1 Introduction

Extrinsic mortality is an important selective agent influencing the evolution of life-histories, prey morphology and behavioural adaptations (Roff 1992; Newton 1998; Caro 2005). In many species, predation is a major contributor to extrinsic mortality, both directly (Caro 2005; Valcu *et al.* 2014) and indirectly, through the trade-off between the time allocated to foraging and the investment in anti-predator behaviours (Kaitala, Lindström & Ranta 1989; Stankowich & Blumstein 2005). Group-living allows individuals to reduce both the predation risk and the costs of antipredator behaviours through several independent mechanisms (Krause & Ruxton 2002a; Caro 2005): It enhances predator detection (Bertram 1978), increases foraging efficiency by reducing individual vigilance (Pulliam 1973), and during a predator attack, provides further benefits through risk dilution (Hamilton 1971) and the confusion effect (Miller 1922).

A large number of field studies have demonstrated that living in groups provides ample antipredator benefits (Caro 2005). Nevertheless, the importance of different causes of mortality remain poorly understood in most animal species, limiting our understanding of the impact of different selective forces on the evolution of group-living (Krause & Ruxton 2002a; Caro 2005). Juveniles (i.e., fledged individuals during their first year of life) typically have higher mortality than older individuals (Sullivan 1989; Newton 1998), which is often a consequence of higher predation risk for juveniles (Covas *et al.* 2004; Gruebler & Naef-Daenzer 2010; Tarwater & Brawn 2010). In animals with slow body growth, such as fish, reptiles and mammals, the high juvenile mortality may be a consequence of an increased predation pressure on smaller individuals (Werner & Hall 1988). In species where individuals rapidly reach adult body size, such as birds, high juvenile mortality may reflect low phenotypic quality, leading to selective disappearance of low quality individuals (Naef-Daenzer, Widmer & Nuber 2001), or age-dependent social dominance where adults are dominant over juveniles (Sullivan 1989). Acting in synergy with the former mechanisms, juveniles may lack foraging (Marchetti & Price 1989) or antipredator skills (Griffin 2004; Griesser

& Suzuki 2016a), increasing their mortality. Because group-living constitutes an effective way for the social acquisition of life-skills (van Schaik & Burkart 2011), it may have been promoted by ancestrally high predator-induced mortality, particularly in inexperienced juveniles.

Here we use data from our long-term study on the Siberian jay (*Perisoreus infaustus*) to investigate the causes of mortality and how social, individual and environmental factors influence mortality. This bird species lives in cohesive groups occupying year-round territories in boreal forests across the Northern Palearctic (Griesser, Nystrand & Ekman 2006b). In addition to the dominant breeding pair, groups can include up to five related and unrelated non-breeders, from up to three different cohorts (mean group size=3.05, range 1-7) (Ekman & Griesser 2016a). About 40% of pairs breed successfully each year (Eggers *et al.* 2006) and in successful broods, socially dominant offspring expel their subordinate siblings from the parental territory 1-2 months after fledging (Ekman, Eggers & Griesser 2002). Subordinate siblings disperse and settle into other groups mostly as non-breeders while dominant juveniles remain on the parental territory up to three years beyond independence (Griesser *et al.* 2014). Parents provide retained offspring with access to food (Griesser 2003), safe locations during foraging (Nystrand 2006; Nystrand 2007), and increased antipredator protection during predator encounters (Griesser & Ekman 2004; Griesser & Ekman 2005). This nepotistic antipredator protection has been suggested to reduce the mortality of retained offspring during their first winter (Griesser, Nystrand & Ekman 2006b).

Against this background, we first describe the variation in predator encounter rates in summer (March-August) and winter (September-February, i.e. the two periods of the year when we surveyed the survival of radio-tagged individuals) across our study sites (see below). Secondly, we use Cox proportional hazards models to investigate how social (rank, group size, group composition, kinship), individual (sex, age, individual condition, body size) and environmental factors (habitat structure, predator abundance) influence mortality (see Table 4-1 for a descriptions of our models and detailed definitions of all parameters). We assessed mortality with

the help of radio-tags. This method provides an unbiased assessment of causes of mortality if all deceased individuals are recovered, as was the case in this study.

Based on an earlier study, we hypothesize that non-breeders and individuals living in managed, more open territories experience a higher mortality than breeders and individuals living in unmanaged territories with a high degree of visual cover respectively (Griesser, Nystrand & Ekman 2006b). Since males exhibit more risky behaviours, for example during predator mobbing (Griesser & Ekman 2005), we predict that they experience higher mortality than females (Nystrand *et al.* 2010). Also, individuals in smaller groups are expected to experience a higher mortality than individuals in larger groups (Roth, Lima & Vetter 2006), and higher predator encounter rate should increase mortality rates. Finally, we investigated the factors that are specifically associated with breeder and non-breeder mortality to also assess the role of group composition and age (breeders only model) respectively kinship and age (non-breeders only model) on mortality.

4.2 Materials and Methods

Data for this study were collected from a long-term study population of Siberian jays near Arvidsjaur (65°40’ N, 19°0’ E) in northern Sweden (Ekman & Griesser 2016a). Here we use data collected from spring 1996 to autumn 2004, and from spring 2011 to autumn 2013, including survival data on 371 individuals from 75 territories. All birds in the study population were individually colour-ringed (Griesser *et al.* 2012), with the exception of 5 individuals. Blood (50 µl) was taken from all individuals for molecular sex (Griffiths *et al.* 1998) and kinship (Griesser *et al.* 2015) determination. Radio-tagging, blood sampling and handling of birds were performed under the license of the responsible ethics board (Umeå djurförsöksetiska nämd: license number A80-99, A45-04, A 50-11).

Table 4-1. Description of the predictors considered in this study. sqrt: square root transformed factors, ID: individual; obs: number of radio-tagging events; N events = number of deceased individuals.

Predictors	Description	Predictions
age	minimum age of focal individual; breeder only and non-breeder only models	juveniles are predicted to have a lower survival than older individuals
feather quality	the maximum number of faulty growth bars found on a single wing feather	juveniles with a high maximum number of faulty growth bars in wing feathers have a reduced survival (Griesser, Nystrand & Ekman 2006b)
group composition	breeder only models: groups without non-breeders, groups include only immigrants, groups include at least one retained offspring	breeders in kin groups may have increased survival due to nepotistic antipredator investment
group size	size of group during the surveyed period; if several birds were radio-tagged simultaneously and one bird died in the first half of the period the other bird was followed, we excluded the deceased bird for the group size count of the second bird	individuals in larger group should experience higher survival due to risk dilution, enhanced vigilance or the confusion effect
habitat structure	proportion of unmanaged forest on each territory	hawks locate jays more easily in open territories, increasing the predation risk (Griesser & Nystrand 2009)
kinship	non-breeder only models: retained offspring, immigrant	retained offspring have a higher survival than immigrant non-breeders (Griesser, Nystrand & Ekman 2006b)
phenotype	breeder only models: retained individuals; immigrants; unknown dispersal timing (see methods)	retained individuals have a higher survival than immigrants (Ekman & Griesser 2016a)
predator encounter rate	Average daily encounter rate of predators in the managed and unmanaged part of the study site in summer and winter	a high predator encounter rate is predicted to reduce survival
rank	breeder; non-breeder	breeders are predicted to have a higher survival than non-breeders
season	summer (survival followed between March and August), winter (survival followed between September and February	more predators are present at the study site during the summer half of the year, lowering the survival
sex	female; male	males take more risks than females and thus, are predicted to have a lower survival than females
tarsus length	tarsus length in mm	larger individuals could have a higher survival

4.2.1 ASSESSMENT OF HABITAT STRUCTURE

Forests at the study site are typical for the boreal zone of northern Europe and cover a gradient from intensely managed to pristine forests (Griesser & Lagerberg 2012). In managed forests, the entire understory (small spruces, deciduous trees) is removed every 20-40 years to enhance timber production. These forests are therefore more open and provide less visual cover than unmanaged forests, increasing the risk for juveniles of being killed by predators (Griesser, Nystrand & Ekman 2006b). Forests in the northern part of the study site are largely unmanaged (referred to as "unmanaged part" hereafter), while forests in the southern part of the study site cover a gradient from clear-cuts, plantations, thinned forests to a few unmanaged patches (referred to as "managed part" hereafter). We used this binary categorization in the analyses concerning the predator encounter rates (see below). In the survival analyses, we included the habitat structure as continuous variable and measured the proportion of unmanaged forest patches that had not been affected by forestry for at least 50 years (Griesser & Nystrand 2009).

4.2.2 ASSESSMENT OF PREDATOR ENCOUNTER RATES

We recorded all predators of Siberian jays that were observed throughout the study period (N=2300 full days in the field): accipiter hawks (goshawk *Accipiter gentilis*, sparrowhawk *A. nisus)*, owls (hawk owl *Surnia ulula*, boreal owl *Aegolius funereus)*, and pine marten *Martes martes*. Since it was not possible to assess which hawk or owl species had killed a jay, we use predator categories (i.e., hawk, owl, marten) instead of specific predator species. We assessed the daily predator encounter rate in both the managed and unmanaged part of the study site during the two periods of the year when we radio-tagged birds (summer, winter). The predator encounter rates were calculated by dividing the number of encountered predators by the sampling effort in both parts of the study site during a study period (i.e., total number of days spent in each part of the study site, correcting for the number of surveyed territories). Given the large home-range of the main

predators and the low predator encounter rates, using number of predators encountered on each territory would not be meaningful.

4.2.3 MORTALITY ASSESSMENT AND PREDATOR IDENTITY

We assessed mortality in Siberian jays with the help of radio tags (Holohil BD-2G, Telenax TBX-006, weight 1.8-2.0g, corresponding to 2.0-2.5% of a bird's body mass) glued to the two central tail feathers or mounted with a leg-loop harness (Rappole & Tipton 1991). We mounted tags in March (years 1996-2004, 2011-2013), June-July (years 2000, 2003, 2011, 2013) and in September-October (years 1999, 2001-2004). The tags usually worked for 14-19 weeks, allowing the monitoring of mortality during this period. Tags mounted on the tail dropped off naturally with the next moult, at a maximum of 8 months after initial fitting. Birds that had the tag mounted with a leg loop harness were recaptured at the end of the surveying period to remove the radio tag. In total, we attached 586 radio-tags on 371 different individuals. While 238 individuals were tagged once, 75 individuals were tagged twice, 43 individuals three times, 10 individuals four times, 1 individual five times and 4 individuals were tagged six times over their lifetime. Individuals tagged in summer were located weekly, while individuals tagged in winter were located at maximum every 7 weeks. In winter, remains of deceased individuals were usually buried in snow and therefore remained intact for long periods. Thus, we could identify predator identity and approximate when the individuals were killed (based on how much snow had fallen after the event) even when the remains were located 2 months after the predation event had occurred. Once the remains of a killed individual were found, predator identity was assessed in the field based on the way the predator handled the prey and the location of the kill (Griesser, Nystrand & Ekman 2006b; Griesser 2013). Hawks pluck their prey on the ground or on an exposed branch (Ferguson-Lees *et al.* 2001), and faeces, foot or wing prints in the snow help to confirm hawk kills. Owls pluck their prey perched up in dense trees (König, Weick & Becking 2009) and in most cases we found characteristic pellets (i.e., regurgitated matter consisting of the indigestible remains of

the prey) among the remains of the killed bird. Martens leave characteristic bite marks on feathers and colour rings.

4.2.4 ASSESSMENT OF GROUP SIZE, KINSHIP AND AGE OF INDIVIDUALS

Groups were visited repeatedly, both before and after attaching radio-tags, by attracting the birds at established feeding sites, and when monitoring the survival of radio-tagged individuals. During these visits, we recorded the identity of all individuals present. Siberian jay groups are very stable and group members move mostly as a cohesive unit through their territory (Griesser, Nystrand & Ekman 2006b), and readily visit established feeding sites (Ekman & Griesser 2016a).

We assessed the kinship of individuals using three methods. In most groups (N=271 broods) we monitored the reproductive success by following reproduction and banding all nestlings in successful broods (see Eggers *et al.* 2006 for detailed description of methodology), therefore allowing us to recognize retained offspring. Otherwise, we caught fledglings 1-3 weeks after they had fledged and banded them before dispersal (N=27 broods). This then meant that all unbanded individuals in these groups had immigrated from elsewhere. Finally, in groups where we did not follow reproduction (N=130 broods), we assessed relatedness of unbanded group members with molecular methods (details given in Griesser *et al.* 2015). Most individuals were ringed as nestlings or juveniles, and thus their age was known, while unbanded juveniles can be reliably aged using the shape of the outermost tail feather (Svensson 2006). The exact age of individuals that were banded as adults (N=98 breeders, N=2 non-breeders) was unknown, and thus we assigned them an age of 2 years at the time they settled in the study population.

4.2.5 ASSESSMENT OF FEATHER FAULT BARS AND BODY SIZE

An earlier study showed that juvenile Siberian jays with a high number of faulty growth bars in their wing feathers had a higher risk of being killed by a predator (Griesser, Nystrand & Ekman 2006b). Faulty growth bars are growth deficiencies (Grubb 2006) that often lead to feather

breakage, which in turn impair manoeuvrability and reduce their escape speed during a predator attack (Williams & Swaddle 2003). We counted the number of fault bars on all wing feathers in the field when attaching the radio-tags, and used the tally from the wing feather with the most faulty growth bars in the analyses. We only counted fault bars that covered at least 50% of the feather width. We used the adult tarsus length of all individuals as a proxy for body size (measured with dial callipers to the nearest 0.1mm).

4.2.6 STATISTICAL ANALYSIS

Statistical analyses were carried out in R version 3.2.2 (R Core Team 2016). We assessed the effect of season (summer, winter; categorical variable) and habitat type (managed, unmanaged; categorical variable) and their interaction on the predator encounter rate using a generalized linear mixed model with a Poisson error distribution and the log link function in the stats package (R Core Team 2016). We included year (categorical variable) as random parameter into this model and used the sampling effort (i.e., number of days and number of surveyed territories per season in each part of the study site) as offset. We evaluated the significance of the random effect year using a likelihood ratio test (LRT) where -2*Δ log-likelihood of the model, with and without the random factor year, is tested against a χ^2 distribution with df=1.

The survival probability of radio-tagged individuals was analysed using Cox proportional hazard models in the package coxme (Therneau 2015) and the package survival (Therneau 2014). These models evaluate the hazard function h(t), which indicates the instantaneous risk of mortality at time t, given survival to time t. They do not assume a normally distributed response variable and can deal with censored data. We investigated the correlates of mortality by running models on all individuals (model 1), breeders only (model 2), and non-breeders only (model 3; see Table 4-2 for the models and details on the predictors used). Prior to running the models, we checked each response variable for its distribution and applied an appropriate transformation to obtain approximately symmetrical distributions (see Table 4-2). All continuous variables were

centred (around the mean) and scaled (by the standard deviation) to facilitate the comparison of effects of explanatory variables (Schielzeth 2010).

Table 4-2. Structure of the three Cox proportional hazard models

Model 1	(event,time)=sqrt(predator abundance)+sqrt(habitat structure)+group size+ rank+season+sex+ rank*sqrt(habitat structure); (N = 371 IDs; 586 obs; N =62 events)
Model 2	(event,time)=log(age)+sqrt(predator abundance)+sqrt(habitat structure)+group size+group composition+phenotype+season+sex; (N = 256 IDs; N = 448 obs; N = 38 events)
Model 3	(event,time)=age+sqrt(predator abundance)+log(habitat structure)+log(group size)+kinship+season+sex ; (N = 135 IDs and obs; N = 24 events)

We used the number of weeks an individual was followed from radio-tagging to last observation or the time of death (see above) in a given radio-tagging period as time to event. For the analyses on all individuals and breeders only we ran mixed effect Cox models, using the function coxme in the package coxme (Therneau 2015), including individual identity as a random factor. We evaluated the significance of the random effect using a LRT (see above). Because only three non-breeders were tagged repeatedly, we chose to only included the first radio-tagging event of these individuals in the analyses on non-breeder mortality. Hence, this allowed us to run a simple (no random effect) Cox model using the function cox.ph in the package survival (Therneau 2014). The regression coefficients obtained for each model represent the log change in the hazard function per unit increase of the predictor variable. A negative coefficient indicates increased survival chances with an increasing value of the predictor variable. Again, we evaluated the significance of the predictors using LRT (see above).

Cox proportional hazards model assume that the hazard ratio is constant over time. This assumption was both tested on models excluding the random factor using the cox.zph function in the package survival (Therneau 2014), and by conducting graphical diagnostics. To check for collinearity, we calculated the variance inflation factor (VIF) (Dormann *et al.* 2013) from a linear mixed effect model (all individuals, breeder only analyses) or a linear model (non-breeder only analysis) including all the predictors investigated using the *vif.mer* function

(https://github.com/aufrank/R-hacks/blob/master/mer-utils.R) and the vif function in the package HH (Richard 2016). The mean VIF of all models were less than 2.1, which indicates an acceptable amount of covariance among predictors. It was not possible to include both rank and age into the model 1 including all individuals, given the high covariance between these two predictors.

We assessed the influence of feather quality and body size on mortality by re-running the three survival models on a subset of individuals for which these data were available. We included the maximum number of faulty growth bars in wing feathers at the time of attaching the radio-tag and the tarsus length of an individual into these models.

4.3 Results

4.3.1 PREDATOR ENCOUNTERS

We encountered predators on 128 occasions during the 12 years where we mounted radio-tags (Figure 4-1). Goshawks (N=45) and sparrowhawks (N=41) were the most frequently observed predators, while owls (N=20) were less frequently encountered. We observed only one pine marten but recorded two nests that were predated by this species. Another 19 encounters involved hawk-sized birds of prey, but the species could not be identified. Sparrowhawks are migratory at the study site, and thus, they were only observed between late April and early September. The average daily encounter rate varied between 0 and 0.03 predators per day and territory (mean=0.004; Figure 4-1), and more predators were encountered during winter and in the unmanaged part of the study site (Figure 4-1a)-b); Table 4-3) than during summer and the managed part of the study site. Also, the encounter rate varied substantially between years (Table 4-3).

Table 4-3. Predator encounter rate analysis. Effect of year, season, habitat type and the interaction between season and habitat type on the predator encountered rate. Estimates and standard errors (SE) are presented. Significant effects are highlighted in **bold**. The p-value for the effect of year was tested using a likelihood ratio test (LRT) between a model including vs. excluding year.

	Effect size levels (categ. variables)	**Estimate**	**SE**	**z-value**	**p-value**
intercept		**-6.12**	**0.28**	**-22.10**	**<0.0001**
season	**winter**	0	na		
	summer	**-0.62**	**0.23**	**-2.64**	**0.008**
habitat type	**managed**	0	na		
	unmanaged	**0.84**	**0.30**	**2.81**	**0.005**
season* habitat type	winter*managed	0.00	na		
	winter*unmanaged	0.00	na		
	summer*managed	0.00	na		
	summer*unmanaged	0.00	0.38	-0.01	0.99
Random effect	**Variance**	**SD**	**LRT**	**df**	**p-value**
year	**0.44**	**0.67**	**33.22**	**1**	**<0.0001**

na – not applicable; levels of categories with "na" are the reference levels.

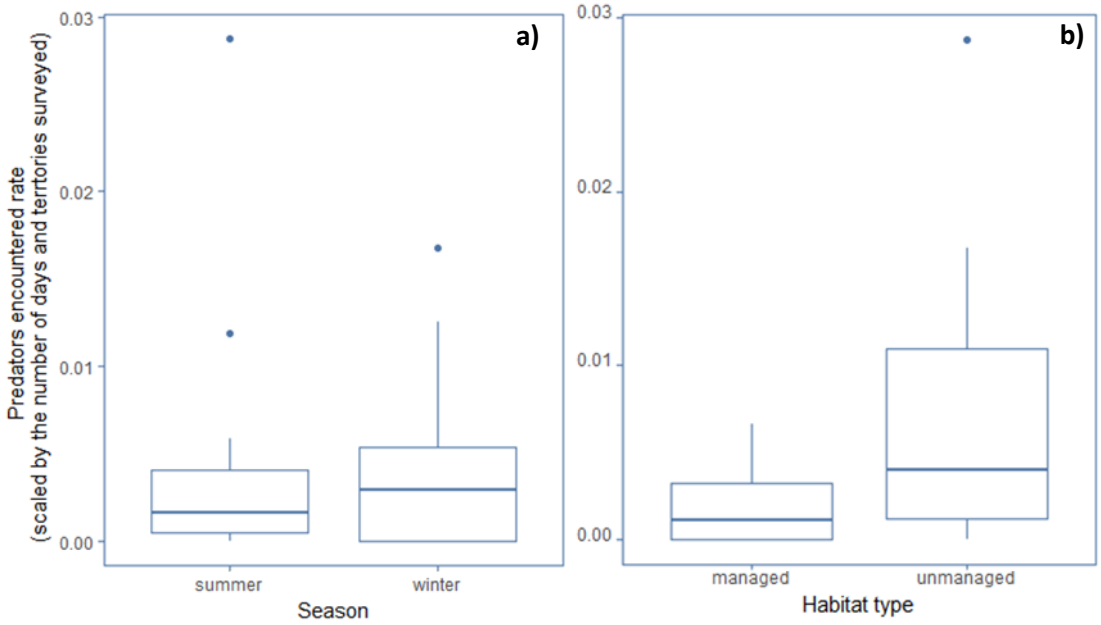

Figure 4-1. Daily predator encounter rate (scaled by the sampling effort) in **(a)** summer (March-August) and winter (September-February; i.e., the two periods of the year where we surveyed the survival of radio-tagged individuals), and **(b)** the managed and unmanaged part of the study site. (line in boxes corresponds to median, boxes to third (up) and first (down) quantiles).

4.3.2 CAUSES OF MORTALITY

All radio-tagged individuals were recovered and 59 out of 62 individuals were the victim of predation. Only 3 individuals (5%) were found dead on the ground without any sign of predation.

Predator category could be identified in 57 cases (97%; Table 4-4): Hawks killed the majority of individuals (N=42 individuals), owls were responsible for 12 kills, and pine martens killed three individuals. Two individuals were killed by an avian predator, but it was impossible to determine whether they were killed by a hawk or an owl.

Table 4-4. Causes of mortality of 371 Siberian jays during 586 tagging periods (shown below in the table). Individuals were followed on average for 13.7 weeks, or until found dead. Three individuals were found dead on the ground between early April and early May without any sign of interactions with predators.

Status	***Number breeders***	***Number non-breeders***
survived	410	114
killed by hawks	24	18
killed by owls	8	4
killed by hawk or owl	2	0
killed by pine marten	1	2
found dead on ground	3	0
total died	38	24
proportion died (%)	8.5	17.3
Total N	448	138

4.3.3 CORRELATES OF MORTALITY

A survival model including all individuals showed that non-breeders had a lower survival than breeders (Figure 4-2). However this effect depended on the habitat structure, and only non-breeders living in more open territories with a low proportion of unmanaged forest had a lower survival than breeders (Figure 4-3). Also, individuals had a comparatively lower survival in winter than in summer (Figure 4-3). Separate analyses for breeders and non-breeders, also including age and rank specific social factors, largely confirmed these results. Among breeders, males experienced a lower survival than females, but no other putative factor influenced their survival (i.e., group composition and size, age or habitat quality; Table 4-5). Among non-breeders, survival was lower on territories with a low proportion of unmanaged forest (Table 4-5). Moreover, older non-breeders had higher survival than juvenile non-breeders (Table 4-5, Figure 4-4), but neither kinship nor group size affected their mortality (Table 4-5). Thus, because non-breeders had higher

mortality rates than breeders, this implies that juveniles had the highest mortality of all age classes. Models that also included feather quality and body size confirmed these findings, but showed that a high number of growth deficiencies in the wing feathers reduced the survival of non-breeders but not breeders (Table 4-6).

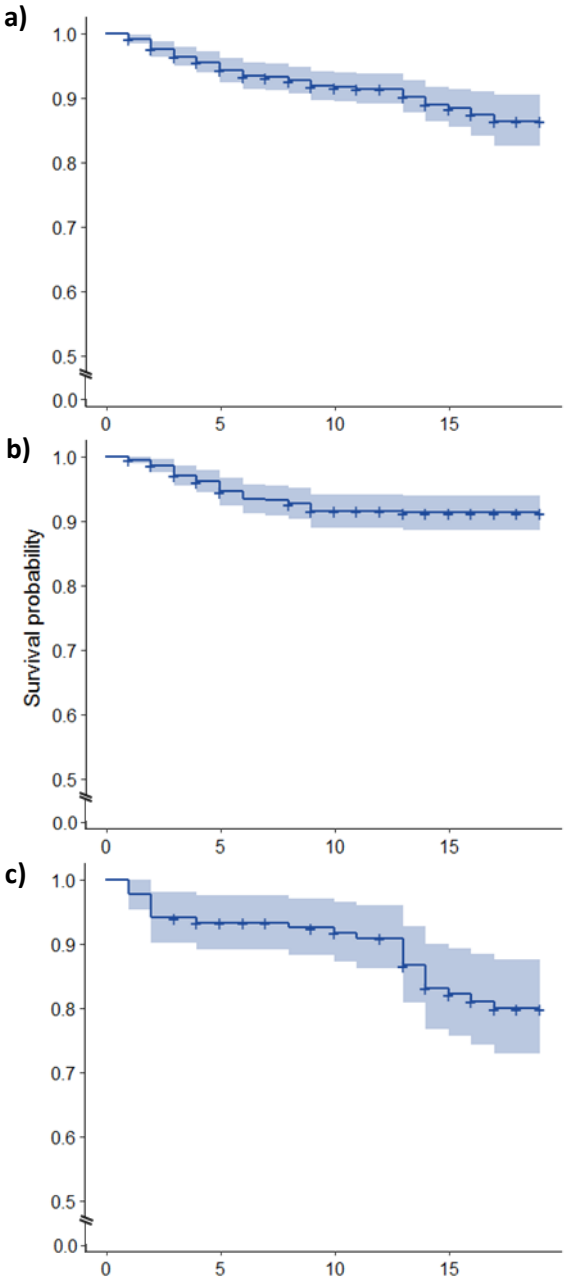

Figure 4-2. Kaplan-Meier survival curves of Siberian jays: all individuals (a), for breeders only (b), for non-breeders only (c). The grey zones indicate the 95% confidence intervals.

Table 4-5. Survival Analyses: (a) all individuals, (b) breeders only, and (c) non-breeders only. Significant effects are highlighted in **bold**. Note that a higher estimate corresponds to a lower survival rate. NB = non-breeders, sqrt = square root transformed factor, log = log transformed factor.

	Effect size levels	Coeff	SE (coeff)	Hazard ratio	X2	DF	p-value
a) all individuals:							
sqrt(predator encounter rate)		0.01	0.16	1.01	2.10	1	0.15
group size		0.05	0.15	1.05	0.99	1	0.32
sqrt(habitat structure)		**-0.03**	**0.17**	**0.97**	**5.97**	**1**	**0.01**
rank	breeder	0.00	na	0.00	1.29	1	0.26
	non-breeder	-0.16	0.41	0.85			
season	**winter**	**0.00**	**na**	**0.00**	**4.03**	**1**	**0.04**
	summer	**-0.58**	**0.40**	**0.56**			
sex	female	0.00	na	0.00	1.13	1	0.59
	male	0.36	0.30	1.43			
sqrt(habitat structure)*rank	**breeder**	**0.00**	**na**	**0.00**	**6.76**	**1**	**<0.0001**
	non-breeder	**-0.85**	**0.35**	**0.43**			
b) breeders only:							
log(age)		0.12	0.18	1.13	0.78	1	0.38
sqrt(predator encounter rate)		-0.09	0.19	0.91	0.16	1	0.69
group size		0.23	0.30	1.26	0.35	1	0.56
sqrt(habitat structure)		0.01	0.18	1.01	0.07	1	0.79
phenotype	kin	0.00	na	0.00	0.50	2	0.78
	non-kin	0.33	0.55	1.39			
	unknown	0.01	0.55	1.01			
sex	**female**	**0.00**	**na**	**0.00**	**4.10**	**1**	**0.04**
	male	**0.77**	**0.4**	**2.17**			
group composition	no NB	0.00	na	0.00	0.34	2	0.84
	kin NB	-0.44	0.75	0.65			
	nk NB	-0.29	0.59	0.75			
season	winter	0.00	na	0.00	0.00	1	0.96
	summer	-0.04	0.75	0.96			
c) non-breeders only:							
age		**-8.00**	**2202**	**0.00**	**4.15**	**1**	**0.04**
sqrt(predator encounter rate)		0.08	0.32	1.08	0.03	1	0.87
log(group size)		0.16	0.23	1.18	0.15	1	0.70
log(habitat structure)		**-0.68**	**0.21**	**0.51**	**12.95**	**1**	**<0.001**
sex	female	0.00	na	0.00	0.08	1	0.78
	male	0.08	0.42	1.09			
kinship	kin	0.00	na	0.00	1.63	1	0.20
	non-kin	0.46	0.44	1.58			
season	winter	0.00	na	0.00	1.05	1	0.31
	summer	-0.64	0.65	0.53			

Table 4-6. Survival Analyses including feather quality and tarsus length: (a) all individuals, (b) breeders only, and (c) non-breeders only. Significant effects are highlighted in bold. Note that a higher estimate corresponds to a lower survival rate. NB = non-breeders, sqrt = square root transformed factor, log = log transformed factor.

	Effect size levels	Coeff	SE (coeff)	Hazard ratio	X2	DF	p-value
a) all individuals:							
sqrt(predator encounter rate)		-0.59	0.30	0.55	1.03	1	0.31
group size		**-0.49**	**0.20**	**0.61**	**11.44**	**1**	**0.0007**
sqrt(habitat structure)		0.54	0.29	1.71	3.73	1	0.053
rank	breeder	0.00	na	0.00	3.35	1	0.07
	non-breeder	0.42	0.54	1.52			
season	**winter**	**0.00**	**na**	**0.00**	**5.69**	**1**	**0.017**
	summer	**-1.11**	**0.59**	**0.33**			
sex	female	0.00	na	0.00	0.40	1	0.53
	male	0.19	0.43	1.21			
tarsus length		0.00	0.19	1.00	0.00	1	0.99
feather quality		0.24	0.15	1.27	2.06	1	0.15
sqrt(habitat structure)*rank	breeder	0.00	na	0.00	1.74	1	0.19
	non-breeder	-0.50	0.37	0.61			
b) breeders only:							
log(age)		0.31	0.28	1.37	0.18	1	0.68
sqrt(predator encounter rate)		-0.59	0.32	0.56	1.01	1	0.31
group size		0.67	0.41	1.95	3.35	1	0.07
sqrt(habitat structure)		-0.15	0.29	0.86	0.22	1	0.64
phenotype	kin	0.00	na	0.00	4.42	2	0.11
	non-kin	2.06	1.21	7.83			
	unknown	0.95	1.19	2.59			
sex	female	0.00	na	0.00	2.75	1	0.10
	male	1.10	0.89	3.01			
group composition	no NB	0.00	na	0.00	4.31	2	0.12
	kin NB	-0.99	1.16	0.37			
	nk NB	0.48	0.87	1.61			
season	winter	0.00	na	0.00	0.03	1	0.86
	summer	-0.22	1.24	0.80			
tarsus length		0.14	0.32	1.15	1.22	1	0.27
feather quality		-0.31	0.39	0.73	0.72	1	0.40
c) non-breeders only:							
age		-3.48	1074.85	0.03	0.97	1	0.33
sqrt(predator encounter rate)		-0.25	0.38	0.78	1.27	1	0.26
log(group size)		0.20	0.23	1.22	0.34	1	0.56
log(habitat structure)		**-1.18**	**0.37**	**0.31**	**17.13**	**1**	**0.00003**
sex	female	0.00	na	0.00	0.00	1	0.98
	male	0.02	0.50	1.02			
kinship	kin	0.00	na	0.00	2.46	1	0.12
	non-kin	0.66	0.45	1.93			
season	winter	0.00	na	0.00	0.29	1	0.59
	summer	-0.41	0.78	0.67			
tarsus length		0.08	0.26	1.08	0.10	1	0.75
feather quality		**0.68**	**0.23**	**1.97**	**8.21**	**1**	**0.004**

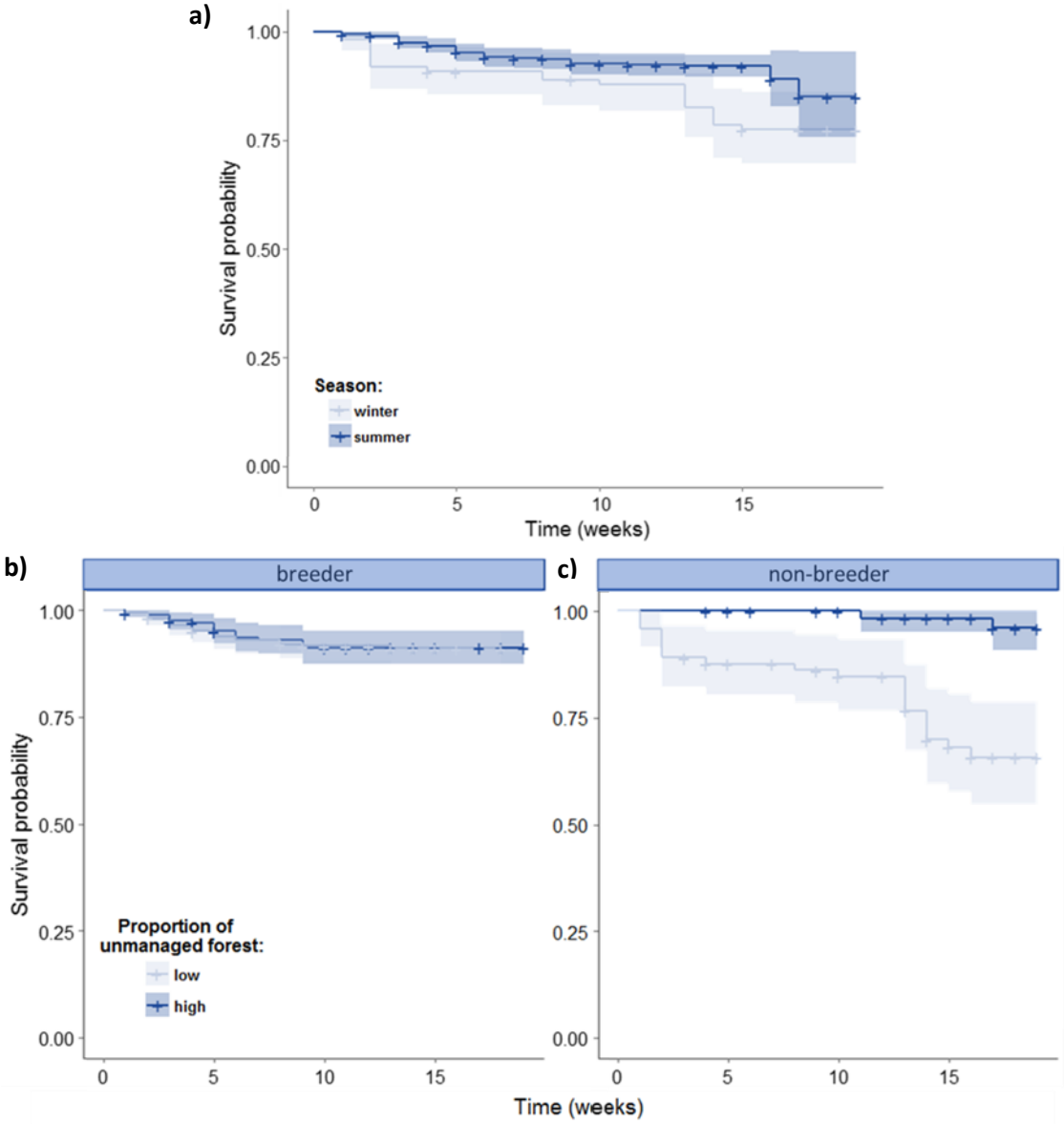

Figure 4-3. Kaplan-Meier survival curves of all birds depending on **(a)** the season, and the interaction between rank (breeder: **(b)**; non-breeders **(c)**) and habitat structure (displayed as binary variable based on a median-split method). The grey zones indicate the 95% confidence intervals.

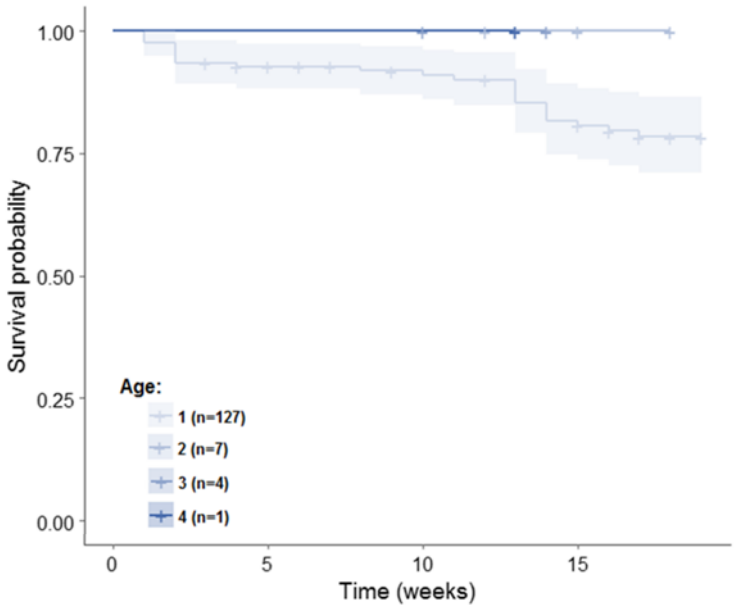

Figure 4-4. Kaplan-Meier survival curves of non-breeders depending on their age. The grey zones indicate the 95% confidence intervals.

4.4 Discussion

Our results show that predation was the primary cause of mortality of 371 radio-tagged Siberian jays, with only 3 out of 61 individuals found dead without signs of predation. These findings confirm the critical role of predation as a source of extrinsic mortality in birds (Newton 1998; Caro 2005; Valcu *et al.* 2014). Other studies highlighted that disease is an important cause of mortality in many species (Scott 1988), including birds (Newton 1998). However, we only exceptionally observed individuals that appeared to be sick, and in only one case did this lead to that the individual disappeared (MG pers. observation). Notably, juveniles had substantially higher mortality than older non-breeders and breeders, but only in managed territories with little visual cover. Similarly, a low feather quality was associated with a high mortality only in juveniles. These findings suggest that older individuals are able to cope with living in more open territories and a low feather quality either because of experience or social dominance, or that juveniles that die are of low phenotypic quality, leading to the selective disappearance of low quality individuals.

The main predators of Siberian jays, *Accipiter* hawks, are visual ambush hunters (Kenward 1978) and locate prey more easily in open forests. In our population hawk attacks were only observed in managed territories (Griesser & Nystrand 2009) and during attacks, these forests provide less cover to escape. Nevertheless, living in territories with little cover increased mortality only in juvenile jays. Juveniles do not respond to hawk models when exposed to them in absence of older individuals (Griesser & Suzuki 2016a), and during simulated hawk attacks, juveniles have a longer reaction time than breeders (Griesser 2013). However, all juveniles that observe knowledgeable group members mobbing a goshawk model survived their first winter (Griesser & Suzuki 2017). These findings support the notion that the high juvenile mortality reflects a lack of antipredator skills. Thus, observing knowledgeable individuals interacting with predators may be critical for naïve Siberian jays, particularly if predators are rarely encountered, as the case in our study population (Figure 4-1).

In addition to lacking predator recognition skills, juveniles may also suffer from a higher mortality due to low social rank or low phenotypic quality. Particularly immigrant juveniles behave in a more risk-prone way than older group members and retained juveniles (Griesser 2003; Nystrand 2006). However, kinship did not influence non-breeder mortality (Table 4-4), and thus, a low social rank *per se* does not increase mortality in Siberian jays. In contrast, low feather quality (i.e., a measurement of phenotypic quality) was associated with a higher mortality of non-breeders (Table 4-5). This difference may be explained by at least two non-exclusive mechanisms. First, a low feather quality increases feather breakage, impairing flight manoeuvrability during predator attacks (Williams & Swaddle 2003). Second, it may reflect a generally low phenotypic quality, whereby low quality individuals might be slower to respond during a predator attack (Cresswell *et al.* 2003). Unfortunately, it was not possible to assess the state of wing feathers in most killed individuals since we rarely retrieved all wing feathers. We repeatedly captured juveniles that survived their first winter of life with broken feathers, suggesting that feather breakage alone does not account for the recorded increase in mortality. Importantly, a low feather

quality did not affect mortality among older individuals, showing that they can cope with this handicap.

In contrast to many other studies (Caro 2005), group size does not influence mortality in Siberian jays. This pattern is remarkable since safety in numbers is particularly efficient in small groups where an additional group member reduces the individual risk substantially more than in larger groups (Roth & Lima 2003; Roth, Lima & Vetter 2006). Given that warning calls during attacks boost non-breeder survival (Griesser 2013), protection by experienced group members may reduce the predation risk of all group members independent of group size. Alternatively, the benefits from safety in numbers may be offset by the costs of living in a larger group, given that predators are more likely to detect a larger group compared to a smaller group (Krause & Godin 1995; Caro 2005). If jays in high-risk, more open habitat were found to live in larger groups, habitat-specific predation rates could be obscuring the link between group size and mortality rates. Yet, our analyses show that group size and habitat structure were independent of each other (VIF for both factors smaller than 1.8).

4.4.1 CONCLUSIONS

Insights into the causes of mortality are important in understanding demography and the evolution of life-history traits (Stearns 1992). Our results support the notion that mortality in birds is largely driven by predation (Newton 1998; Valcu *et al.* 2014), and highlight that experience has a large impact on mortality (Marchetti & Price 1989; Mumme *et al.* 2000; Schuppli *et al.* 2012). Species that live in predator free environments, such as seabirds, experience low extrinsic mortality (Valcu *et al.* 2014), contributing to their extraordinary long lifespans and associated slow life-history pace (Mourocq *et al.* 2016). Yet, individuals in species that regularly encounter predators on their own have a high risk of being killed, making individual learning difficult (van Schaik 2010). Group living can directly provide safety in numbers (Caro 2005) but may also provide inexperienced individuals with a safe haven to acquire critical life-skills (van Schaik & Burkart 2011;

Loukola *et al.* 2013; Griesser & Suzuki 2017). Finally, living in habitats that provide protection from predators can buffer the predation risk of inexperienced individuals, which may explain the accelerated population declines of many species living in managed habitats, not only in the tropics but also in boreal forests (Monkkonen 1999; Eggers & Low 2014; Virkkala 2016). In a number of bird species, juveniles have a high mortality in more open habitats (Cox *et al.* 2014b), leading to population declines in these habitats (Sisk *et al.* 1994; Davies, Margules & Lawrence 2000). Thus, changing forestry management strategies away from clear-cutting and thinning regimes, towards more green continuous forestry practises (Gustafsson, Kouki & Sverdrup-Thygeson 2010) is likely to improve juvenile survival in forest dwelling species, and hence, have potentially large positive effects on their population dynamics.

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Concluding remarks

Summary of results

CHAPTER 1 – AGE AT FIRST REPRODUCTION

Fitness can be profoundly influenced by the age at first reproduction (Cole 1954; Caswell 1982). To date, the relationship between the age at first reproduction and fitness only has been investigated intraspecifically (see references in Table 1-S1) and results are equivocal. In **Chapter 1**, I provide a first comparative analysis using averaged within-species data to examine interspecific variation in the relationship between age at first reproduction and lifetime reproductive success. Age at first reproduction varies both within and among species. On average, long-lived species have later age at first reproduction than short-lived species. The variation in age at first reproduction within and among species is reflected also in lifetime reproductive success. In most species, an early or a late onset of reproduction is associated with a decrease in lifetime reproductive success. Furthermore, the species-specific age at first reproduction that results in the highest lifetime reproductive success was related with the age at sexual maturity, allowing me to assess the differences in the benefits and costs associated with variable timing in the onset of reproduction among species. A delayed age at first reproduction (beyond the age at sexual maturity) is beneficial in large and long-lived species, and in species where early age at first reproduction is associated with a decrease in subsequent survival or reproductive output.

The most frequently observed age at first reproduction within a species results in the highest lifetime reproductive success. It has been argued that constraints on reproduction, such as the availability of high-quality mates or breeding sites, influence the evolution of a delayed onset of reproduction (Emlen 1982; Koenig *et al.* 1992; Arnold & Owens 1998; Hatchwell & Komdeur 2000). Thus, the findings from **Chapter 1** suggest that a delayed onset of reproduction

is an optimal strategy facilitated by a long lifespan rather than a “best of bad job” strategy (Covas & Griesser 2007). The decrease in lifetime reproductive success and future survival linked to an early age at first reproduction may reflect costs of reproduction of inexperienced individuals. Contrary to mammals where the age at first reproduction is determined by energetic constraints, the time required to learn adult-level foraging skills is limiting the onset of reproduction in birds (Schuppli, Isler & van Schaik 2012). In large or long-lived species, the time needed to acquire the experience that is sufficient to survive and reproduce successfully might be higher, explaining that a delayed onset of reproduction is beneficial in species with increased body mass and long lifespan.

Overall, the results from **Chapter 1** provide the first empirical confirmation of key predictions of life-history theory across species that lifespan and costs of reproduction shape reproductive timing (Lack 1968; Roff 1992; Stearns 1992; Charlesworth 1994). Additionally, **Chapter 1** challenges current theories on the evolution of family formation and cooperative breeding.

CHAPTER 2 – PARENTAL CARE DECISIONS TO RISKS

A central issue in life-history theory is the trade-off between survival and reproduction (Roff 1992; Stearns 1992). Its balance varies among species, but the reason for this variation remains largely unknown (but see Ghalambor & Martin 2000; Ghalambor & Martin 2001). Parental care responses to predation risks during the period of nestling provisioning are short-term, with potential long-term fitness consequences (Lima 2009; Zanette *et al.* 2011). While comparative studies on parental decisions to diverging risks of predation have the potential to provide greater inferences into the evolution of parental investment strategy, such studies are rare. In **Chapter 2,** I fill this gap by assessing how an increased perceived risk of predation to adults or nestling in 12 bird species changed the nest visitation behavior of parents. It reveals that species decrease their nest visitation rates only in the presence of a predator of adults but not a nestling predator, suggesting

that breeding parents tend to favour their own survival over the condition of their offspring. This finding adds to the body of evidence demonstrating that birds can adjust their reproductive strategies depending on the type of risk in ecological time (Lima 2009; Hua et al. 2014). However, it contrasts with previous studies that found a decrease in nest visitation rate under an increased nest predation risk (Eggers, Griesser & Ekman 2005; Martin & Briskie 2009; Zanette *et al.* 2011; Ghalambor, Peluc & Martin 2013; Grunst, Grunst & Rotenberry 2015).

The costs and benefits associated with responses to risks of predation should influence parental care strategies among species, and may depend on their life history, social system and ecology (Montgomerie & Weatherhead 1988; Lima & Dill 1990b; Ghalambor & Martin 2001; LaManna & Martin 2016). **Chapter 2** demonstrates that, under generally increased predation risk, the reduction in nest visitation rate is stronger in species that do not re-nest within breeding seasons, have a short lifespan, or open nests. Contrary to species with a high probability to re-nest within the breeding season or a long life expectancy, species with a low re-nesting potential or a short life expectancy incur high fitness costs from losing their current nest (Roff 1992; Stearns 1992). Species that have open nests have a higher chance of being predated than cavity nesters (Martin & Li 1992). Therefore, the results from **Chapter 2** suggest that the sensitivity to an increased perceived risk of predation is higher in species that pay higher costs of predation. These species may have developed more intense stress-responses to unpredictable perturbations that trigger behavioral changes redirecting energy allocation from breeding to survival ("emergency life history stage": Wingfield *et al.* 1998; but see: Bokony *et al.* 2009). A previous study demonstrated a role for within season re-nesting potential to the evolution of parental care responses to a nest predator during the incubation period. For the first time, **Chapter 2** demonstrates the role of re-nesting potential on parental care responses during the nestling period when parents are at risk, i.e., in circumstances implying a survival-reproduction trade-off for the parents, since responses to risk, such as a reduction in nest visitation rates to improve adult survival, can compromise nestling condition.

Overall, the results from **Chapter 2** show empirically that short- and long-term reproductive prospects, as well as natural vulnerability to risks, are major drivers of parental care responses to predation risk among species. **Chapter 2** further contributes to our understanding of the evolution of parental care strategies in general.

CHAPTER 3 – JUVENILE SURVIVAL AND LONGEVITY

Unusual ratios of juvenile to adult survival could explain uncommon combinations of life-history traits (Kraus et al. 2005). Thus, assessing correlates of unusual juvenile survival-longevity combinations could improve our understanding of life-history evolution. Yet, comparative studies investigating survival across different life stages and the conditions that link with different juvenile survival-longevity associations are lacking. **Chapter 3** helps to fill this gap. In accordance with the life-history theory (Stearns 1992; Charlesworth 1994), it demonstrates that large body size, long incubation period and low annual parental investment, typical of a slow life-history, correlate with a high juvenile survival (i.e., from fledging to age one) and a long lifespan. However, juvenile survival and longevity correlate with different environments that are associated with different risks. Species with open-nest on the ground, and thus with high nest predation risk, have a higher post-fledging survival. Species living in dense habitat and foraging on the ground, and thus with higher adult predation risk, have a shorter lifespan. The former result highlights that nesting habitats, which provide short-term benefits (i.e. a lower nest predation (Martin & Li 1992)), can have negative down-stream effect on juvenile survival that were overlooked so far (but see Martin 2014). Together, these results suggest that the difference in the environments occupied prior to fledging and then later by adults might explain contrasting pattern of juvenile and adult survival.

Juvenile survival is assumed to be positively correlated with longevity ("theory of aging": Williams 1957; Charlesworth 1994; Ricklefs 1998; Kirkwood 2002). However, the results in **Chapter 3** reveal that the combinations of juvenile survival and longevity can greatly deviate from this assumption (about 80% of the species included in this study). The direction of the deviations

is not a function of life history, ecology or social system. However, deviations are generally higher in species with uniparental care, that are habitat generalist, are nocturnal, have a slow life-history or live in habitats with low risks of adult predation. Not all deviations were equivalent. Some species showed unexpected combinations of high first-year survival/long lifespan or low first-year survival/short lifespan. These deviations are consistent with a positive correlation between juvenile survival and longevity. However, some species have combinations that contradict this positive correlation, showing unexpected combinations of high first-year survival/short lifespan or low first-year survival/long lifespan. The results of **Chapter 3** reveal that for those deviations that contradict theory, the direction of the deviation mattered. Species that express high deviation towards high first-year survival/short lifespan have a short lifespan, live in stable environments, breed cooperatively, have precocial young and a specialized diet, while the reverse was partly true for species with high deviation towards low first-year survival/long lifespan.

Overall, **Chapter 3** reveals that species with unusual combination of juvenile survival and longevity show consistent differences in their ecological and social traits. The findings imply that interspecific diversity in the relationship between juvenile survival and longevity results from divergent selective pressures. Alternatively, they suggest that divergent age-specific survival is at the origin of the diversity in species attributes, supporting the importance to consider age-specific survival for understanding the evolution of life-history traits (Cole 1954; Williams 1966; Promislow & Harvey 1991; Roff 1992; Charlesworth 1994; Martin 2015).

CHAPTER 4 – SURVIVAL IN SIBERIAN JAY

Extrinsic mortality has a strong impact on the evolution of life-histories, prey morphology, and behavioural adaptations (Roff 1992; Newton 1998; Caro 2005). Additionally, extrinsic mortality of juveniles or adults can affect population dynamics (Clark & Martin 2007). However, for many animals the causes of mortality, especially in juveniles, are poorly understood (Clark & Martin 2007; Robinson *et al.* 2010; Tarwater *et al.* 2011; Cox *et al.* 2014a). Juveniles typically have higher

mortality than older individuals (Sullivan 1989; Newton 1998), which is often a consequence of higher predation risk for juveniles (Covas *et al.* 2004; Gruebler & Naef-Daenzer 2010; Tarwater & Brawn 2010). **Chapter 4** confirms these findings in a group living species from northern Sweden, the Siberian jay *Perisoreus infaustus*. Juveniles have the lowest survival of all age classes, and 95% of death are due to predation (in most cases by *Accipiter* hawks). The latter finding confirms the critical role of predation as a source of extrinsic mortality in birds (Newton 1998; Caro 2005; Valcu *et al.* 2014).

While juveniles Siberian jays have a lower survival in managed habitats with little visual cover and when having feathers of low quality, none of these factors influences the survival of older individuals. These results suggest that older individuals can cope with both factors and highlight that experience can buffer extrinsic mortality (Marchetti & Price 1989; Mumme *et al.* 2000; Schuppli *et al.* 2012). Group living can directly provide safety in numbers (Caro 2005; Roth, Lima & Vetter 2006) but may also provide inexperienced individuals with a safe haven to learn critical life-skills (Griffin 2004; van Schaik & Burkart 2011; Loukola *et al.* 2013; Griesser & Suzuki 2017). Together with the results of a previous study which demonstrates that juvenile Siberian jays learn critical antipredator skills from experienced group members (Griesser & Suzuki 2017), the results from **Chapter 4** support that group living may offer social opportunities for young Siberian jays to learn critical life-skills. This result is in accordance with findings on other bird species or taxa, showing that social learning improves anti-predation behaviors (reviewed in: Griffin 2004). However, in contrast to many other studies (Caro 2005), group size does not influence mortality in Siberian jays. Additionally, in long-lived species, such as the Siberian Jay, younger age classes account for a large contribution to the demographic stochasticity (Sæther et al. 2013). Thus, the lower juvenile survival in managed habitats may explain the accelerated population declines of many long-lived species living in such habitats. **Chapter 4** could have useful implications for conservation management of endangered species.

General conclusion

Survival and reproductive strategies contribute directly to the way in which an organism propagates itself, and are the most important components of fitness (Roff 1992; Stearns 1992). Understanding the diversity of survival and reproductive strategies is therefore a central goal of evolutionary biology. While the influence of ecology and/or the trade-offs between life history traits to understand variation in species-specific life-history traits is well investigated (Roff 1992; Charlesworth 1994; Losos *et al.* 2014), the role of the social system received little consideration. Specifically, few studies assessed the influence of ecology, social system, and life histories together to assess their relative importance in explaining the variation in specific life-history traits. This dissertation tries to fill this gap by investigating the relative association of the variation in survival and reproductive strategies with different ecological and social factors as well as other life-history traits in birds.

Chapter 1 to 4 reveal that age at first reproduction, parental decisions during nestling provisioning, and age-specific survival vary greatly within and among avian species. When it comes to the causes of this variation, this dissertation reveals **(i)** that age-related experience plays an important role in reproductive strategies and survival in birds in accordance with previous studies (Marchetti & Price 1989; Forslund & Pärt 1995; Part 1995; Mumme *et al.* 2000; Schuppli, Isler & van Schaik 2012) (**Chapter 1** and **3**). Furthermore, this dissertation emphasizes that the acquisition of experience is more likely to influence reproductive strategies in larger and long-lived species, and that sociality may influence the acquisition of experience, more specifically boosting juveniles survival (Figure C). **(ii)** The results of this dissertation highlight that longevity is an important force in the evolution of avian breeding biology (**Chapter 1** and **2**). Specifically, **Chapter 1** provides an empirical demonstration that lifespan influences fitness costs associated with early reproduction (i.e., well-established life-history paradigm: Roff 1992; Stearns 1992) and in turn explains variation in reproductive strategies (Figure C). **(iii)** This dissertation reveals that different sets of life-history,

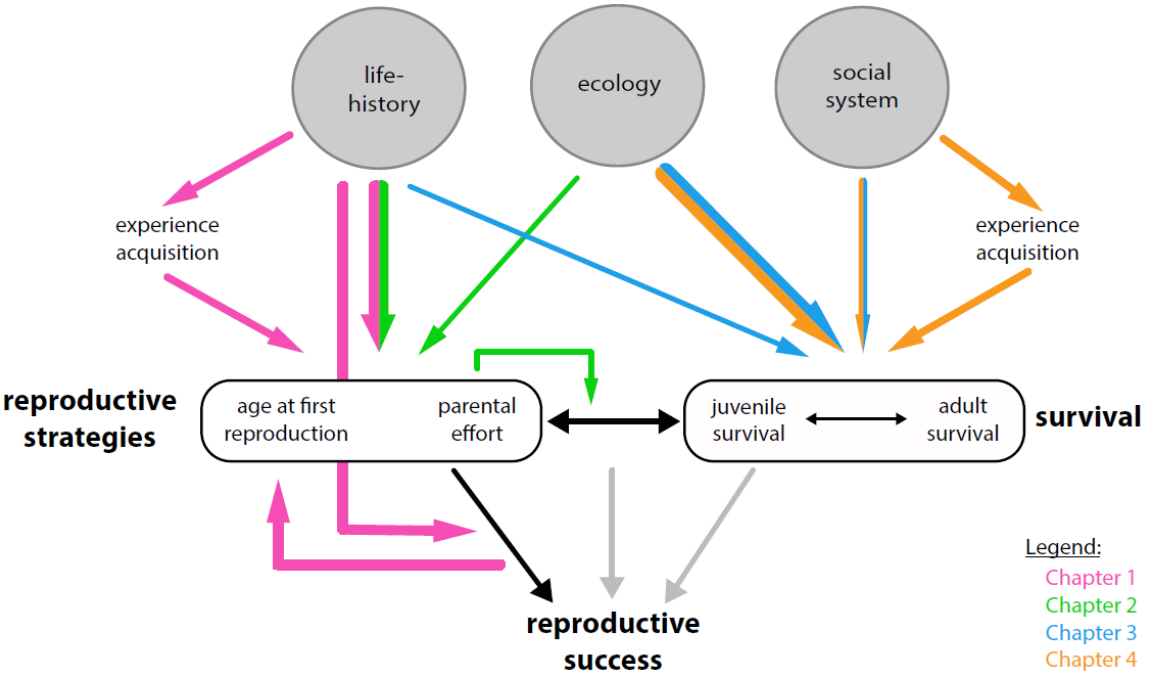

Figure C: Main predictors of reproductive strategies and survival. While mainly life-history and few ecological factors influence reproductive strategies, survival is principally influenced by the ecological and social environment. See chapters for the direction and magnitude of the effects. Grey arrows means: not addressed in this dissertation. The thickness of the colourful arrows reflects the importance of the effect. See Appendix B for more details on the predictors involved.

ecological and social factors correlate with juvenile survival, adult survival, and with different combinations between the two (**Chapter 3** and **4**). Those findings support that more attention should be given to age-specific survival for understanding the evolution of life-history traits and demography, in accordance with previous theoretical (Cole 1954; Williams 1966; Promislow & Harvey 1991; Roff 1992; Charlesworth 1994) and empirical studies (fish: Reznick, Bryga & Endler 1990; bird: Martin 2002; mammal: Kraus *et al.* 2005; bird: Martin 2015). **(iv)** Altogether, the findings of this dissertation emphasise the crucial role of short- and long-term reproductive prospects, as well as costs of reproduction on reproductive strategies in birds. Social and most ecological factors do not play a major role (Figure C and Appendix B) (**Chapter 1** and **2**). In contrast, they reveal that social and ecological factors account for most of the variation in survival both within and among species (Figure C and Appendix B) (**Chapters 3** and **4**). Ultimately, this dissertation clarifies the source of variation in reproductive strategies and age-specific survival and contributes to a better understanding of life-history evolution. Because age-specific survival

and reproductive strategies are important demographic attributes, identification of patterns in their variation can have direct application in conservation biology (Dobson & Lyles 1989; Saether, Ringsby & Roskaft 1996; Caro 1998; Festa-Bianchet & Apollonio 2013). Thus, this dissertation may also help in the management of endangered species.

Further Perspectives

Chapter 1 reveals that the cost of early reproduction explains optimal delayed onset of reproduction. An interesting path for future investigation would be to study the correlates of the cost of early onset of reproduction. One way to do so could be to use a linear mixed effect model including our "before variation index" (index assessing the relationship between age at first reproduction and lifetime reproductive success prior to the species optimal onset of reproduction) as response variable, and similar or enlarged set predictors than the ones used in **Chapter 1**. Although the results from **Chapter 1** reveal no significant effect of sex, the relationship between age at first reproduction and lifetime reproductive success and the optimal timing of reproduction sometimes differed between sexes (Figures 1-3 and 1-S4). Previous study highlighted the need to consider sex-specific variation in life-history traits (McDonald 1993; Santos & Nakagawa 2012). Hence, further investigation of sex-specific differences in reproductive strategies and their impact on fitness would be valuable. A detailed species by species analysis of directional and stabilizing selection on age at first reproduction would also be an interesting path for future investigation. I plan to do so on the few species from **Chapter 1** for which the detailed data required for such an analysis are available as well as additional species by contacting researchers susceptible to have such detailed data.

Despite the large number of studies on parental care responses to risk, relatively little is known about the temporal patterns of parental care behaviours in different risk situations. The way the visits to the nest are spread over time under increased predation risks can differ greatly and reveals divergent parental trade-off between survival and reproduction. Hence, a valuable

extension of **Chapter 2**, would be to assess temporal pattern in the nest visitation behaviour by determining, for instance, intervisit interval (Mutzel *et al.* 2013). It could allow to detect behaviour developed to compensate for the decrease in visitation rate and hence, improves the interpretation of the findings from **Chapter 2**. Response of the parents to the presence of predators should diminish over time owing to adaptive habituation (Rankin *et al.* 2009). If compensation behaviour for the detrimental effect on nestling exists (Eggers et al. 2005), we could expect to see an increase in visits' frequency by the end of the exposure session. Assessing the synchronisation of the visits by the parents (Raihani *et al.* 2010; van Rooij & Griffith 2013) and food load per visits (Eggers, Griesser & Ekman 2008) would also be useful; however, the data from **Chapter 2** allow us to investigate the latter only on few species. Additionally, unlike nest predation, predation on parents has received little attention, and its potential as a major determinant of parental care decision has been largely unappreciated. Therefore, we emphases the need for more studies assessing parental care responses in ecological time to a risk on adult only (Lima & Dill 1990a).

My PhD was part of an ambitious project carried out in strong collaboration with my colleague Gretchen Wagner. Even if not fully reflected by this dissertation, it involved five years of intense fieldwork on more than 12 bird species during which, together with teams of field assistants, we monitored their reproduction and realized several experiments. Empirical studies, already in the process for publication, examine the source of interspecific variation in **(i)** reproductive allocation strategies when faced with increased nest predation risk prior to egg-laying and the downstream effects on breeding success (see pages 231 to 256), and **(ii)** parental care responses during provisioning of nestlings to an experimentally increased cost of caring for offspring resulting from the handicapping of one parent (see pages 257 to 287). Results reveal that the duration of parent-offspring association and the demand of parental care (e.g. high demand in large species with long care periods) affect early reproductive allocation decisions and parental care decisions during the nestling period, respectively.

Data still remain to be analysed, which might open the door for many more interesting studies. For instance, I am currently working on the results from a comparative empirical field study which aims at understanding parental care strategies during the incubation period. Similarly to the experiment of **Chapter 2**, we increased the perceived risk of predation on the egg and the adults respectively and recorded the change in parental behaviours. Specifically, I will investigate nest attentiveness and alertness of the incubating individual, but also feeding behaviour from the other individual as such feeding events can alter the trade-off between survival (leaving the nest to forage) and reproduction (staying at the nest to take care of the eggs) faced by the incubating individual. Because the requirements for parental care and reproductive value of eggs and grown nestling might be different, I expect a shift in parental behavioural decision over the course of the breeding cycle. Comparing the results of such study with the one from **Chapter 2** will provide a greater understanding on the evolution of parental care strategies.

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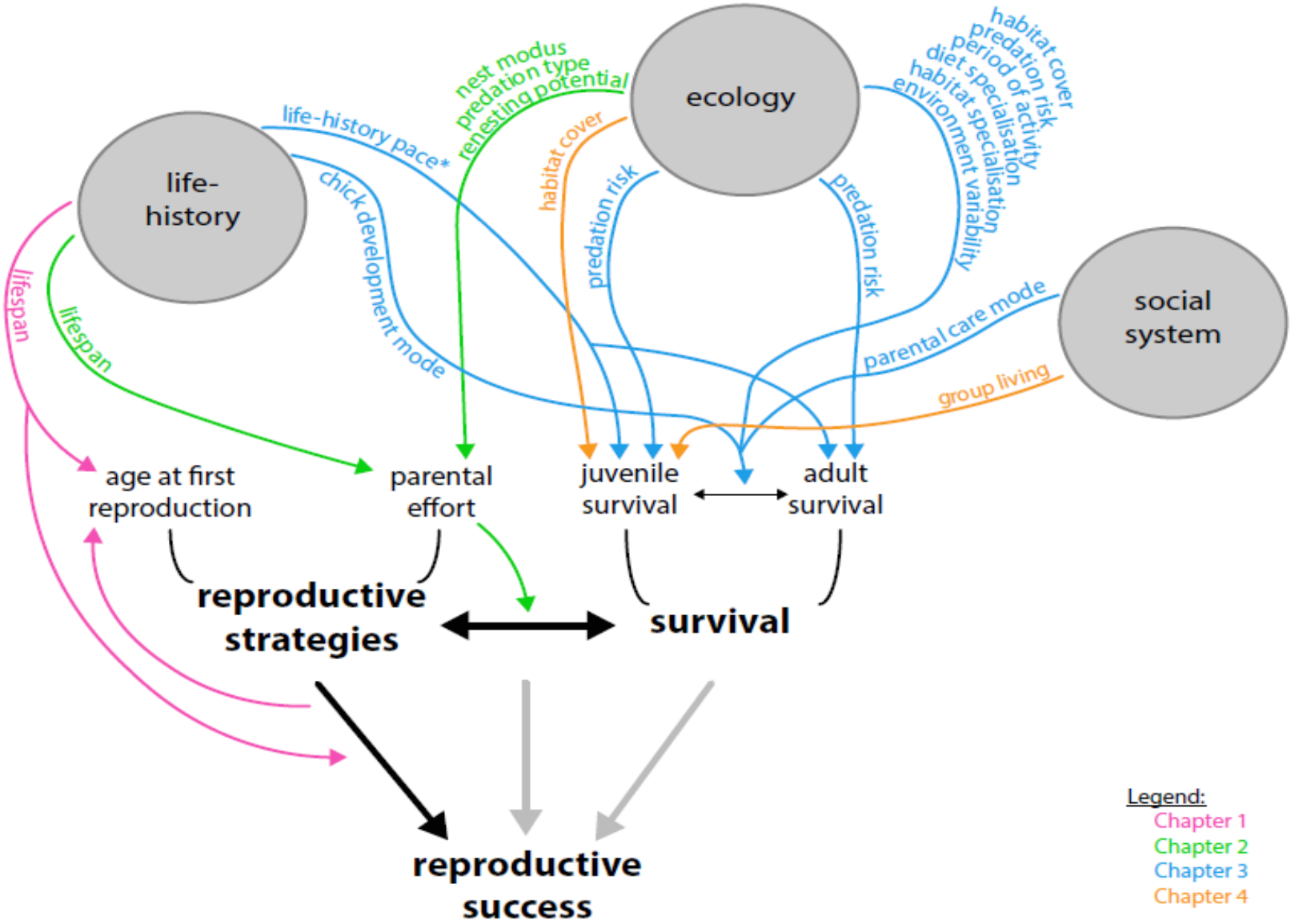
Appendix

Appendix A: List of the social, ecological and life-history factors considered within each chapter to investigate the variation in reproductive strategies or survival.

Appendix B: Main predictors of reproductive strategies and survival revealed by this dissertation.

Appendix A: Factors considered in each chapter to investigate the variation in reproductive strategies and survival. Detailed predictions for each predictors are given within the chapters. Appendix B gives a summary of the main predictors of this variation.

	Chapter	Ecological	Social	Life-history
Inter-specific	**1: onset of reproduction**	- geographic latitude - nest location (as an index of nest predation risk)	- family-living (yes, no) (Drobniak *et al.* 2015) - helper presence (yes, no)	- developmental mode (precocial, altricial) - mean lifespan - adult body weight - age at physiological maturity
	2: parental care responses to predation risks	- nest type (cavity or open nester) - nest predation rate - within season re-nesting potential - daily precipitation - daily temperature	- post fledging parent-offspring association time	- adult body weight - maximum longevity - brood size
	3: first-year survival and maximum longevity	- sedentariness - period of activity (nocturnal, diurnal) - number of avian predators - nest location and type (as an index of nest predation risk) - vegetation cover - foraging area (as an index of exposure to predator) - foraging strategy (as an index of foraging cost) - habitat (specialist, generalist) - diet (specialist, generalist) - caloric content food - fibre content food - mean duration growing season - geographical region	- parental care mode (uni-, bi-parental care, cooperative breeding) - family-living (yes, no) (Drobniak *et al.* 2015)	- adult body weight - body-scaled annual parental reproductive investment (egg mass*number of eggs per clutch*number of successful clutch per year]/body mass; Sibly *et al.* 2012) - incubation period - nestling period - developmental mode (pecocial, non-precocial)
Intra-specific	**4: survival of breeders and non-breeders**	- proportion of managed forest - predator encounter rate	- group size - group composition - social rank (breeder, non-breeder; retained, immigrant)	



Appendix B: Main predictors of reproductive strategies and survival. While mainly life-history and few ecological factors influence reproductive strategies, survival is principally influenced by the ecological and social environment. See chapters for the direction and magnitude of the effects. Grey arrows means: not addressed in this dissertation. * correspond to body size, incubation and nestling period, and reproductive investment ([egg mass x number of eggs per clutch x number of successful clutch per year] / body mass).

Further work to which I contributed during my PhD

Perceived nest predation risk prior to breeding influences reproductive allocation strategy and nesting success in birds

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Abstract

Offspring predation is the primary source of reproductive failure in many species and the mere fear of offspring predation can shape the evolution of reproductive decisions. Yet, it remains unclear why phenotypic responses to an increased risk of offspring predation vary across species, and if temporary changes in risk prior to a reproductive attempt have downstream effects on breeding success. Here we temporarily increased the perceived risk of nest predation prior to egg-laying in eight bird species to assess interspecific variation in risk-dependent changes to reproductive allocation and success. Contrary to prevailing theory, there was no clear pattern of a reduction to clutch size across species, however clutch volume and nesting success were generally reduced under an increased perceived risk. Furthermore, species with a prolonged parent-offspring association increased their within-clutch variation in egg volume. This novel finding suggests that birds may diversify their reproductive allocation under a high perceived nest predation risk, and highlights that the duration of parent-offspring association can affect early allocation decisions. We demonstrate that a temporary change in predation risk at a critical moment of reproductive decision-making can have delayed consequences on fitness, emphasizing that rapid temporal variation in predation risk may favor the evolution of reproductive flexibility in birds.

Introduction

Predation of eggs or dependent young is a major cause of reproductive failure, affecting the evolution of reproductive allocation (Ricklefs 1969, Martin 1995, Martin and Briskie 2009). The mere fear of predation can influence the behavior, condition, fitness, and population dynamics of prey, sometimes even surpassing the lethal effects of direct predation (Lima 1998, Preisser et al. 2005, Cresswell 2008). Therefore, fear of offspring predation may critically shape reproductive decisions to decrease the probability of offspring mortality (Creel and Christianson 2008, Martin and Briskie 2009). However, the benefits derived from fear can be offset by costs, such as reduced reproductive success, even in the absence of direct predation (Preisser et al. 2005, Zanette et al. 2011).

Natural predation risk is ubiquitously variable and can change rapidly over time and space. Consequently, field studies have investigated changes in parental decisions over natural risk gradients (Zanette et al. 2006, Thomson et al. 2011) and in response to experimental modifications of perceived risk (Fuller and Berglund 1996, Ghalambor et al. 2013). In birds, field experiments have demonstrated that parents can alter their reproductive investment depending on the perceived nest predation risk (Eggers et al. 2006, Zanette et al. 2011, Hua et al. 2014). However, these single-species investigations have yielded contrasting results, suggesting that species differ in their responses (Ibáñez-Álamo et al. 2015), which was confirmed by a recent comparative study (LaManna and Martin 2016). These studies increased the perceived risk of nest predation from before egg-laying until after offspring fledging (Zanette et al. 2011, Hua et al. 2014, LaManna and Martin 2016; but see Eggers et al. 2006), providing insights into the influence of generally high or low predation risk on reproductive investment and success. However, anti-predator responses can depend on the frequency and duration of high-risk situations (Lima and Bednekoff 1999, Ferrari et al. 2009), and it remains unknown if temporary increases in risk levels early in a reproductive cycle have downstream effects on reproductive decisions and reproductive success. The initial reproductive allocation sets the upper limit for the number of

offspring produced, and must be weighed against the effort it will require to raise the offspring and the probability of their survival. A temporary increase in the perceived risk to forthcoming offspring prior to egg-laying may therefore have detrimental effects on the success of that reproductive event.

Here we investigated differences in the reproductive responses of eight bird species to an experimentally increased perceived risk of nest predation prior to egg laying. We examined how life-history and ecological factors influence the risk sensitivity of an individual in ecological time. Comparative experimental studies such as this one face an important challenge: it is preferable that all study species are confronted with identical stimuli. However, this approach does not always result in a comparable stimulus among species. For example, a common jay (Garrulus glandarius) is a common nest predator of open nests but does not pose a risk to the nests of cavity-breeding species. Thus, to compare the response of species which vary in their life history and ecology, we used the predator(s) which represent a high risk for each species. In most cases these predators were avian, and we used vocalizations to simulate their presence. However, in two of our study species (*Oenanthe leucura, Merops apiaster*) we rarely or never observed nest predation by avian predators, and so we presented live, confined rats (*Rattus norvegicus*) as the stimulus. This design generates important caveats: different predator types (e.g., mammalian vs. avian) may in themselves present different risks due to diverse hunting techniques and behavior, and the structure of the stimulus (auditory only vs. auditory + visual) may elicit different responses. Therefore, to ensure that differences in responses were not based on the stimulus type *per se,* we include the stimulus type as a factor in all analyses. Furthermore, in many small bird species, rats present a risk to adults as well as offspring, however in the species studied here we have never observed a rat predating an adult on the nest (throughout several years of video recording), and we know of no cases reported in the literature (Soler et al. 1995, Petrescu and Costica 2001).

Following life-history theory, we expect that species with a slow life history pace are the most sensitive to adverse breeding conditions (Roff 1993, Erikstad et al. 1998), and consequently reduce

their allocation in a risky environment. The plasticity of responses to nest predation risk should also vary depending on the level of risk (Ghalambor et al. 2013, LaManna and Martin 2016), thus species with naturally high nest predation rates and more vulnerable nest structures are expected to be most sensitive to an experimental increase in the perceived risk of predation. Furthermore, species with extended post-fledging parent-offspring association (i.e., family-living, Drobniak et al. 2015) are predicted to lay smaller eggs when faced with high nest predation risk, as these species have a greater opportunity to compensate for poor offspring condition than species with prompt offspring dispersal.

A widespread response to variable and/or unpredictable environments is an increased variance in investment across offspring (Crump 1981, Koops et al. 2003, Marshall et al. 2008). In birds, within-clutch differences in egg size can result in a hierarchy among nestlings (Slagsvold et al. 1984, Arnold 1991), allowing parents to selectively raise the strongest offspring if poor conditions persist, but maintain the possibility of raising all offspring if conditions improve (Lack 1947). Birds often reduce the provisioning rate to nests in the presence of nest predators (Eggers et al. 2005, Ghalambor et al. 2013, Schneider and Griesser 2015), and birds breeding in unpredictable environments particularly neglect offspring in poor condition (Caro et al. 2016). Based on these ideas we speculated that female birds may also increase the variance in egg size in response to variable nest predation risk (Hussell 1972), but this hypothesis has not been previously tested.

Material and Methods

STUDY SPECIES AND SITES

Data for this study were collected from seven bird species in Southern Spain in 2011-2014 and one species in Northern Sweden in 2004 (Table 1). In Spain, the experiment was conducted in populations of great tits (*Parus major*) and spotless starlings (*Sturnus unicolor*) near Cordoba (37°95’N, 4°40'W), black wheatears (*Oenanthe leucura*), European bee-eaters (*Merops apiaster*), red-billed choughs (*Pyrrhocorax pyrrhocorax*) and long-tailed tits (*Aegithalos caudatus*) near Guadix (37°25’N, 3°05’W),

and common blackbirds (*Turdus merula*) near Lecrín (36° 56'N, 3° 33'W). Siberian jays (*Perisoreus infaustus*) were studied near Arvidsjaur in Northern Sweden (65°40'N, 19°7'E). For this species, we used previously published data (Eggers et al. 2006), including only the data from the year that the experimental design corresponded with the one used in Spain. To ensure that fundamental differences between the species studied in Spain and Sweden do not drive our findings, we re-ran our analyses excluding the Siberian jay, which yielded analogous results (Tables S3-S6).

Table 1. Study species differ in life history and ecology. 'N pred.' is the number of nests in the predator treatment group and 'N cont.' is the number of nests in the control group. 'Time in nest' is the average number of days from egg laying until fledging, 'post-fledging time' is the average number of days spent in association with parents after fledging.

species		**experiment**			**species traits**							
common name	**scientific name**	**N pred**	**N cont**	**year**	**body mass (g)**	**adult survival (%)**	**nest type**	**no. of broods**	**mean clutch size**	**nest time (d)**	**post-fledging time (d)**	**nest predation (%)**
Black wheatear	*Oenanthe leucura*	8	9	2012	36	49.5	closed	2.5	4.0	31	200	28.6
Common blackbird	*Turdus merula*	8	19	2011	94	56.0	open	2.5	2.9	27	21	21.7
European bee-eater	*Merops apiaster*	11	12	2013-2014	52	49.8	closed	1.0	5.7	57	250	22.8
Great tit	*Parus major*	10	10	2012	17	48.6	closed	1.5	7.5	37	30	36.9
Long-tailed tit	*Aegithalos caudatus*	9	11	2013	7	55.0	open	1.0	7.3	32	300	77.8
Red-billed chough	*Pyrrhocorax pyrrhocorax*	13	16	2013-2014	310	80.0	closed	1.0	4.7	56	42	7.7
Siberian jay	*Perisoreus infaustus*	9	9	2004	84	69.0	open	1.0	3.9	42	400	15.6
Spotless starling	*Sturnus unicolor*	13	8	2012	74	49.9	closed	2.0	4.6	34	7	26.3

EXPERIMENTAL DESIGN

We manipulated the perceived risk of nest predation by simulating an increased presence of nest predators in nesting areas prior to egg laying. We selected common nest predators for each species based on multiple years of nest monitoring. For each species, nesting areas were randomly assigned to either a predator treatment group or a control group while balancing the sample sizes. For the

predator treatment of open-nesting species (Table 1) we play-backed calls of locally occurring corvids (*Pica pica*, *Garrulus glandarius, Corvus corone, Corvus corrax)*, for closed-nesting species whose principal nest predators are avian, we played calls of woodpeckers (*Dendrocopos major, Picus viridis)*, and for two closed nesting species (black wheatear, European bee-eater) whose nest predators were mainly small mammals or snakes, we presented a live brown rat (*Rattus norvegicus*) in a transparent plastic box. The control treatment consisted of a playback of locally occurring non-threatening species' calls (pigeons: *Columba palumbus* and *Streptopelia turtur,* or songbirds: *Turdus merula* and *Carduelis chloris*) or presence of a harmless mammal (European rabbit, *Oryctolagus cuniculus*).

Playbacks in Spain were presented daily from 07:00-19:00, with 12 hours of silence played overnight. Each 12-hour period of calls was comprised of a unique combination of 15-30 seconds of calls, separated by 4 minutes of silence. Calls were downloaded from www.xeno-canto.org. Each playback unit was comprised of a box with battery, amplifier, speaker, and mp3 player, and was placed on the ground, covered with a camouflage cloth. Live animals were kept in the territories continuously. All nests were visited every 1-3 days to maintain the treatments (change batteries, care for animals) and to check nest contents. The locations of playbacks and mammals were changed during each visit. The details of the playbacks used for Siberian jays can be found in Eggers et al. (2006); the only difference in the set-up was that territories were only exposed every second day to playbacks due to field logistics.

Nest areas were determined through three methods. The experimental location was based on previous nests for species with consistent nest locations across years (black wheatear, red-billed chough, Siberian jay) or nests were located early in the construction phase (long-tailed tit, European bee-eater, great tit). For two densely nesting species (common blackbird, spotless starling), we placed playbacks throughout the study area and subsequently located nests that were within the area the playbacks were audible (mean nests per playback: common blackbird=2.08, spotless starling=1.75). Across all species, playbacks were located a mean distance (±SE) of 43±2.5m from the nests. Mammals

were located 26±1.5m from the nests. We began the experiment approximately 10 days prior to egg laying in all species, which was estimated based on the phenology of previous breeding seasons and/or nest-building progress. On average, nests were exposed for 9.6±0.14 days. The treatments were removed within three days of the onset of egg laying (mean time between start of exposure and onset of egg laying=8.2 days).

Once a clutch was complete, we measured the length and width of all eggs using dial calipers (0.1mm accuracy). Individual egg volume was calculated using the formula $volume=0.51*(length)*(breadth)^2$ (Hoyt 1979). Nests were monitored throughout the breeding cycle. The number of eggs, hatchlings and fledglings, and any nest failures, were recorded for each nest. The number of fledglings was assessed based on the number of nestlings in the nest prior to fledging (<3 days) and/or observations of juveniles after fledging. Nest failures were assumed to be caused by predators if: (i) predation was documented through direct observation or recording, (ii) the entire clutch or brood disappeared prematurely, or (iii) evidence, such as punctured eggs, or albumen or blood on nest material, was discovered. We were unable to identify the source of other nest failures, but causes may include nest abandonment, parental death, parasitism, starvation or adverse weather.

STATISTICAL ANALYSES

All statistical tests were conducted with R 3.1.0 (R Core Team 2014). Because many life-history traits within a species are correlated (Stearns 1992), we ran a principal components analysis (PCA; package 'psych', Revelle 2015) on continuous species traits of interest (adult survival probability, body mass, nesting time, and post-fledging parent-offspring association time; see Table 1) to identify significant combinations of these traits and to create new uncorrelated variables. We relied on the correlation matrix among variables (Table S1) to generate PCA scores rather than the covariance matrix (Graham 2003) because the units of measurement for traits differed. The inspection of a scree plot and eigenvalues (package 'nFactors', Raiche 2010) suggested the extraction of 2 components. We first

performed an oblique (oblimin) rotation of the components to simplify the factor structure by maximizing the variances of loadings, which indicated that the resulting factors were not correlated (r=-0.11). We then applied a varimax rotation to the original components. Differences in results of the rotation techniques were negligible, and did not influence the pattern of loadings, so we retained the oblimin rotation in further analyses (Kieffer 1998). The two components extracted from the PCA cumulatively accounted for 89% (60 and 29%, respectively) of the total variance in the included species traits. The first component, labelled “life-history pace”, included adult body mass, nesting time (from egg-laying until fledging), and adult survival (Table S1). High values of this component represent large-bodied, long-lived, slow-developing species. The second component, labelled “time post-fledging”, included only the post-fledging association time of offspring with their parents (Table S1).

To examine among-species patterns of experimental effects on clutch size, egg volume, clutch volume, within-clutch variation of egg volume, number of hatchlings and number of fledglings we ran separate (generalized) linear mixed models (GLMM; package 'nlme', Pinheiro et al. 2014). All models initially included the experimental treatment (predator, control), nest type (open, closed), natural predation risk (percent of non-experimental nests lost to predation in the year of the experiment), number of broods (species-average number of successful broods per year), and the two PCs (life-history pace, time post-fledging) as explanatory variables. Relative laying date (the number of days since the first egg of the year for each species), stimulus type (mammalian, avian), and mean distance between each nest and the experimental stimuli were included as potential covariates. The interactions between the experimental treatment and each of those factors were also included in initial models. Clutch size was included as a covariate for all models except that of clutch size itself. Year and species identity were included as random factors in all models, and nest identity was additionally included as a random factor in the model of egg volume.

Only completed clutches were included in these analyses. We were unable to obtain egg measurements in some nests due to nest inaccessibility or early egg breakage (n=19 across species)

and those nests were excluded from analyses of egg or clutch volume (see Table S3 for sample sizes). Clutch volume was log-transformed prior to analyses. Continuous variables were scaled to unit variance and centered to facilitate the comparison of effects of multiple explanatory variables (Schielzeth 2010). Models of clutch size, number of hatchlings and number of fledglings were fitted with a Poisson distribution, all other response variables assumed a reasonably Gaussian distribution. Appropriate model fits were confirmed with chi-square tests of the residual deviance and inspection of the residual distributions.

We examined whether nests were more likely to fail or succeed according to the experimentally increased risk of nest predation prior to egg laying. We fit binary (logit link) Markov chain GLMMs (package 'MCMCglmm', Hadfield 2010) for overall nest success, and nest success at each stage of nesting (fail/succeed at egg stage, fail/succeed at nestling stage for nests that hatched at least one egg). The same parameters were used as listed above for the models of reproductive traits. The models were run for 100’000 iterations, with a burn-in period of 2’000 iterations and a thinning interval of 100, which resulted in approximately 1’000 samples from the posterior distributions for each model parameter. We specified an inverse gamma prior, with the random effects variance set as V=1 and nu = 0.002. Residual error was fixed at one. Model convergence was confirmed by visual examination of trace plots and calculation of autocorrelation between iterations.

Non-significant ($p>0.10$) interactions between main effects and main effects were sequentially removed from models to attain a minimal adequate model (Crawley 2002), except the experimental treatment, which was retained in all models. Estimates of non-significant terms were acquired from fitting each non-significant term individually into the minimal model (Crawley 2002). Values for non-significant interactions are not reported.

Results

Analyses were based on 175 nests of eight species (Table 1). Assessment of clutch volume indicated that females in the predator treatment had reduced clutch volume across species, while controlling for significant effects of natural differences related to actual predation risk, relative laying dates, and clutch sizes (Table 2). An increased within-clutch variation in egg volume was associated with prolonged associations between offspring and parents in the nest predator treatment group (Fig. 1), while controlling for a significant effect of the treatment's proximity to the nest (Table 2).

Clutch size was not influenced by the experimental treatment when controlling for significant influences of natural predation risk, number of broods, and nest type (Table 3), nor did any included factor explain interspecific differences in treatment effects. No included factor explained interspecific differences in the treatment effects on egg volume (Table 2).

Table 2. Model estimates and corresponding standard errors and p-values for predictors of allocation into eggs. Significant fixed effects (p<0.10) are denoted in bold. Random effects are standard deviation. est.=estimate, p=p-value.

	egg volume			clutch volume			egg volume variation		
fixed effects	**est.**	**SE**	**p**	**est.**	**SE**	**p**	**est.**	**SE**	**p**
intercept	0.04	0.11	0.73	0.09	0.29	0.75	-0.11	0.18	0.55
treatment (predator)[1]	0.001	0.02	0.97	**-0.05**	**0.02**	**0.04**	0.20	0.14	0.15
life-history pace	**0.97**	**0.13**	**<0.01**	**1.10**	**0.36**	**0.03**	-0.14	0.18	0.44
time post-fledging	0.06	0.18	0.74	0.46	0.44	0.35	-0.03	0.17	0.88
number of clutches	**0.24**	**0.11**	**0.07**	0.50	0.33	0.19	-0.39	0.27	0.21
predation risk	0.07	0.05	0.21	-0.50	0.20	0.24	0.14	0.15	0.36
nest type (open)[1]	0.11	0.25	0.68	-0.09	0.69	0.90	-0.41	0.35	0.31
laying date	**-0.02**	**0.01**	**0.08**	**-0.07**	**0.02**	**<0.01**	-0.06	0.12	0.62
predator type (mammalian)[1]	-0.07	0.27	0.80	0.41	0.72	0.59	-0.12	0.64	0.86
proximity to nest	0.02	0.03	0.44	0.02	0.03	0.60	**-0.49**	**0.17**	**<0.01**
clutch size	0.02	0.02	0.24	**0.34**	**0.02**	**<0.01**	0.10	0.07	0.13
treatment (predator)[2] x number of clutches				**-0.06**	**0.03**	**0.03**			
treatment (predator)[2] x time post-fledging							**0.41**	**0.16**	**<0.01**
random effects									
species	1.59			0.80			0.36		
year	<0.01			<0.01			<0.01		
nest	0.52								

[1] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an estimate of 0.

Table 3. Model estimates and corresponding standard errors and p-values for predictors of the number of offspring at each nest stage. Significant fixed effects (p<0.10) are denoted in bold. Random effects are standard deviation. est. =estimate, p=p-value.

	clutch size			number of nestlings			number of fledglings		
fixed effects	est.	SE	p	est.	SE	p	est.	SE	p
intercept	**1.70**	**0.05**	**<0.01**	**0.41**	**0.15**	**<0.01**	**0.93**	**0.30**	**<0.01**
treatment (predator)[1]	-0.04	0.07	0.55	0.05	0.08	0.55	0.08	0.11	0.44
life-history pace	**-0.12**	**0.05**	**0.02**	0.04	0.04	0.31	0.06	0.05	0.23
time post-fledging	-0.01	0.05	0.79	0.03	0.04	0.53	-0.01	0.06	0.82
number of clutches	**-0.17**	**0.04**	**<0.01**	-0.10	0.08	0.24	-0.16	0.09	0.09
predation risk	**0.23**	**0.04**	**<0.01**	0.000	0.002	0.97	0.002	0.004	0.59
nest type (open)[1]	**-0.39**	**0.09**	**<0.01**	0.02	0.09	0.82	-0.14	0.12	0.25
laying date	0.002	0.04	0.96	-0.002	0.004	0.59	0.001	0.004	0.87
predator type (mammalian)[1]	-0.05	0.09	0.59	0.02	0.10	0.86	0.09	0.13	0.49
proximity to nest	0.02	0.05	0.70	-0.02	0.05	0.64	-0.04	0.06	0.48
clutch size				**0.20**	**0.03**	**<0.01**	**0.13**	**0.04**	**<0.01**
random effects									
species	0.02			<0.01			<0.01		
year	<0.01			<0.01			<0.01		

[1] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an estimate of 0.

Experimental nests tended to be more likely to fail to fledge any offspring than control nests (odds ratio= 2.20, 95% credible interval= 1.07 to 5.37, p=0.06, Fig. 2) when controlling for natural nest predation rates (Table S3). This effect was particularly pronounced during the nestling stage (odds ratio= 3.74, 95% credible interval= 1.15 to 12.43, p= 0.01, Table S3). At the egg stage, only open nesting species in the predator treatment were more likely to experience nest failure (treatment x nest type: odds ratio= 8.94, 95% credible interval= 1.19 to 64.07, p= 0.02), while controlling for natural differences in failure rates between the predator type and post-fledging time with parents (Table S3). These results are unlikely to reflect differences in direct nest predation: the proportion of predated nests did not differ between the experimental and control groups (29.6% vs. 23.7% respectively, N=46 nests, p=0.37). In successful nests, the number of hatchlings (mean weighted effect size=0.01±0.25, p=0.97) and the number of fledglings (mean weighted effect size=0.10±0.27, p=0.71) did not differ

between the treatment groups among species (Table S2), nor did any included factor explain interspecific differences in these responses to the treatment (Table 3).

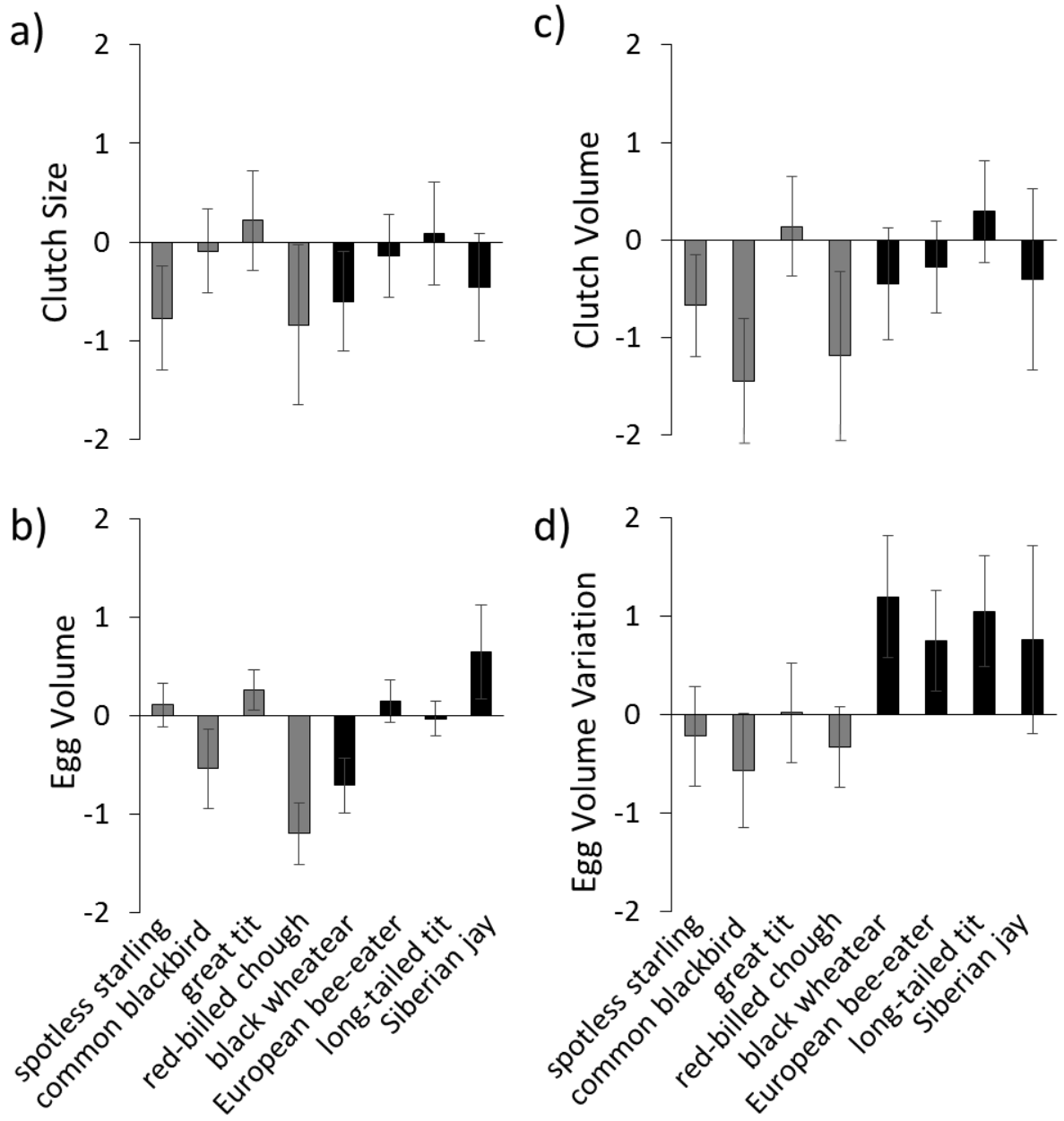

Figure. 1. Reproductive allocation responses to an experimental increase in perceived risk of nest predation prior to egg-laying. Responses are standardized effect sizes (Cohen's d ± 1 SE, Table S2). Negative values reflect a decrease in the treatment group compared to the control group. Species are arranged in order of increasing post-fledging time with parents; grey bars represent non-family-living species, black bars represent family-living species (according to Drobniak et al. 2015). When faced with an increased perceived risk, females either did not adjust, or marginally reduced, **(a)** clutch size and **(b)** egg volume. These factors combined to generate a more general decrease in **(c)** clutch volume. **(d)** An increased within-clutch variation of egg volume (coefficient of variation) was found in family-living species.

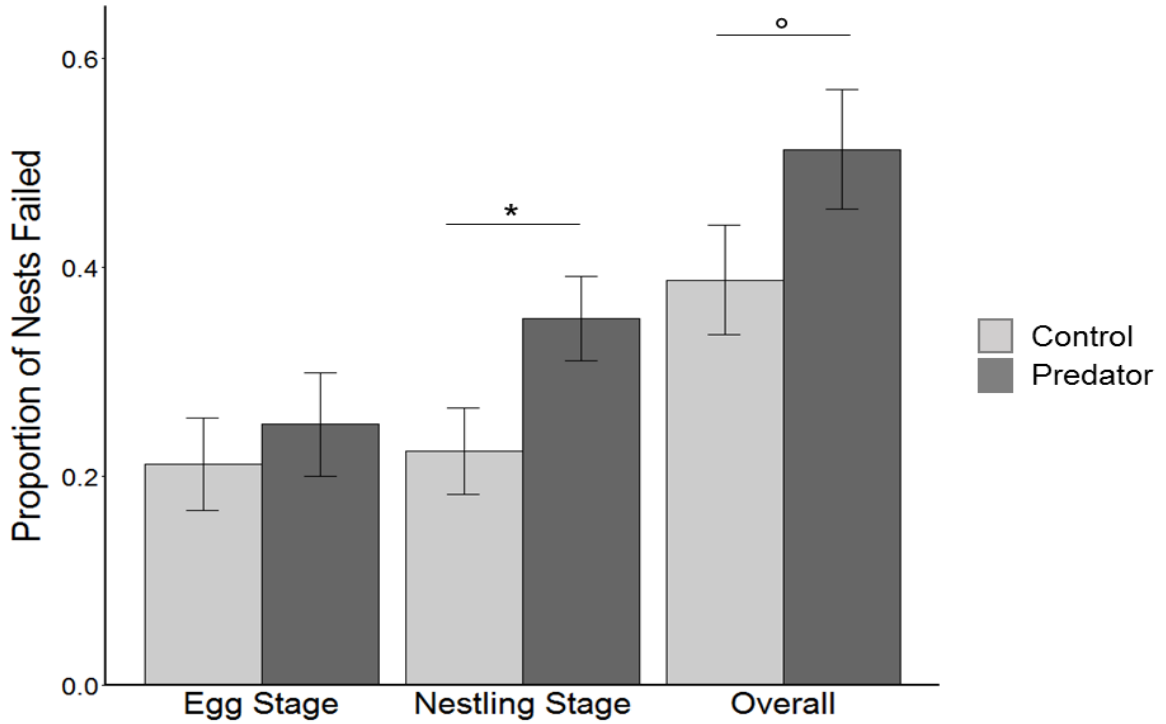

Figure 2. Nests exposed to an increased perceived risk of predation were more likely to fail. Treatment and control means (± 1 SE) at the egg stage, nestling stage, and overall. *p<0.05; °p<0.10.

Discussion

Nest predation is the primary source of reproductive failure in many avian populations and is likely to impose selection for adaptations that reduce nest predation risk and/or the costs associated with nest predation. Our comparative experiment corroborates that species vary in their responses to an increased perceived risk of nest predation (Ghalambor et al. 2013, LaManna and Martin 2016), and demonstrates that a temporarily increased nest predation risk prior to egg-laying can have detrimental downstream effects on reproductive success. In general, birds showed a decrease in clutch volume when faced with an increased risk, a combined effect of minor reductions to clutch size and egg volume. In addition, we show for the first time that birds may respond to a high risk of nest predation by altering the distribution of their reproductive allocation across their eggs, resulting in a marked increase in within-clutch variation of egg volume. This response predictably varied with prolonged parent-offspring association. These findings lend further support to the importance of nest predation in shaping reproductive investment decisions and success in birds (Lima 2009, Ibáñez-Álamo et al.

2015), and highlight that species differ in the strength and nature of their response depending on their post-fledging association with their offspring.

Predation risk can fluctuate considerably over time, and the perceived risk of nest predation early in a reproductive cycle may not reflect the actual risk of nest predation later on. Brood reduction, which is facilitated by variation in egg size (Slagsvold et al. 1984), may be an adaptive strategy to cope with unpredictable environments (Caro et al. 2016). If high predation risk prevails throughout the nesting period, a smaller number of nestlings may reduce the risk of whole brood failure through reduced nest attentiveness (Eggers et al. 2008, Ghalambor et al. 2013). However, if all offspring survive, parents may compensate for offspring condition asynchronies through prolonged post fledging care and/or preferential care of lesser offspring once the high risk period has passed (Shizuka and Lyon 2013). Our results give support to a compensation strategy, as a risk-dependent increase in within-clutch variation in egg volume was only found in species with a long post-fledging parent-offspring association. In these species, parents have a greater opportunity to balance out offspring quality after their offspring have fledged, which may allow for greater flexibility in reproductive allocation. Indeed, species with prolonged parent-offspring association not only have longer durations of post-fledging parental care, but this period can be highly variable and have significant consequences for offspring survival (Green and Cockburn 2001, Griesser et al. 2006).

Theory predicts that breeding birds should decrease their reproductive investment when faced with a high risk of nest predation (Roff 1993). While decreases in clutch size have been found in some experimental studies of individual species (Eggers et al. 2006, Zanette et al. 2011, Hua et al. 2014), neither our investigation nor previous comparative work (Yanes and Suárez 1997, Fontaine and Martin 2006, LaManna and Martin 2016) have found a strong general pattern of clutch size varying with predation risk. Because any change in clutch size is necessarily incremental, this response cannot allow for a fine adjustment of investment. Therefore, continuous changes to egg size may be a more prudent response, considering the unpredictable nature of predation risk (Fontaine and Martin 2006).

Adjustments to egg mass were found in a previous comparative study, however the direction of the responses differed depending on the species' re-nesting potential: species with multiple broods reduced egg mass, while single-brood species increased egg mass (LaManna and Martin 2016). Among the species studied here, we found no general pattern of changes to egg volume, nor were treatment differences in egg volume related to the number of broods or any other investigated factor. More work is required to determine if these patterns differ due to differences in reaction norms, the responses measured, or study design. Nevertheless, we found a general trend of a reduction to clutch volume among the tested species, resulting from joint effects of minor adjustments to egg and clutch sizes. Adjustments to clutch size and egg size are probably variants of the same response (Zanette et al. 2011), and thus the overall effects are most clear when measured as the total combined investment into offspring quantity and quality (i.e., clutch volume).

Nests exposed to an experimental increase in the perceived risk of nest predation prior to egg-laying were less likely to fledge offspring than control nests, particularly due to failure during the nestling stage. There was no difference in the number of fledglings from successful nests, indicating that whole-brood loss was the driving factor for experimental differences in reproductive success. Yet, the proportion of nest failures caused by direct nest predation did not differ between the experimental and control nests, suggesting that other causes of failure were responsible for this difference (e.g., abandonment or starvation). Previous studies have reported decreased reproductive success when the perceived risk of nest predation was high throughout the entire breeding cycle (Zanette et al. 2011, Hua et al. 2014, LaManna and Martin 2016). Consequently, differences in reproductive success have been attributed to combined effects of parental decisions under high risk during egg-laying, incubation and provisioning. Our experimental treatment was removed at the onset of egg-laying, highlighting that the conditions, and resultant investment decisions, at the laying stage can impact reproductive success even if conditions improve. Because risk can be transitory and decisions made under high risk can be costly, it would be adaptive to make substantial adjustments to

behavior only under an immediate threat. Thus, we suggest that the here observed decrease in reproductive success is likely a delayed consequence of reduced investment at the laying stage rather than behavioral changes during offspring rearing.

Surprisingly, reproductive responses to nest predation risk did not vary with life-history pace. Although species with a slow life-history pace are expected to be sensitive to adverse breeding conditions (Roff 1993, Erikstad et al. 1998), our results suggest that phenotypic responses to a high nest predation risk at the time of egg-laying do not differ along a life-history spectrum. Furthermore, we found no relationship between natural predation rates and responses to an artificially increased perceived risk, despite that the few studies which have addressed variation in responses to risk have largely focused on differences in evolutionary histories of predation pressure (Lima and Dill 1990, Relyea 2001, Ghalambor et al. 2013; but see LaManna and Martin 2016). Nevertheless, interspecific differences in clutch size and volume were significantly related to natural predation rates, suggesting that mean levels of predation risk impact the evolution of reproductive strategies but do not influence responses to variation in risk in ecological time. This result corroborates recent claims that risk-dependent reproductive decisions may have a proportionally higher impact on reproductive success in species with generally low predation rates (Creel and Christianson 2008, LaManna and Martin 2016).

In conclusion, our results illustrate that predation risk is an important selective factor influencing avian reproductive decisions among species, yet the mechanisms and consequences of this influence require further attention. In particular, the novel link between within-clutch egg size variation and predation risk highlights that family-living species may use a bet-hedging strategy under high risk conditions. Furthermore, increased nest predation risk at the time of egg-laying had delayed detrimental effects on reproductive success, emphasizing the need for assessment of how variable risk levels at different times during the breeding cycle ultimately affect reproductive success. Finally, these results further demonstrate that responses to nest predation risk prior to breeding are not “one

size fits all" among species, and accentuate the need for additional comparative studies to understand the evolved mechanisms for coping with changes to offspring predation risk and to develop a framework of how other life-history, ecological and/or social factors contribute to interspecific differences.

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Supplementary Material

Table S1. Correlation matrix, standardized principal components loadings, and communality (h2) of continuous species traits. Eigenvalues and cumulative variance explained by each component is given.

correlation matrix					**loadings**		**h^2**
	body mass	time in nest	time post-fledging	adult survival	PC1	PC2	
body mass	1	0.58	-0.39	0.95	**0.93**	-0.25	0.98
time in nest (laying – fledging)	0.58	1	0.14	0.53	**0.82**	0.44	0.78
time post-fledging	-0.39	0.14	1	-0.16	-0.09	**0.95**	0.93
adult survival	0.95	0.53	-0.16	1	**0.93**	-0.07	0.88
eigenvalue					2.44	1.13	
cumulative variance explained (%)					60	89	

Table S2. Odds ratios (OR) and corresponding 95% credible intervals (C.I.) and p-values (p) for predictors of nest failure at the egg stage, nestling stage, and overall nest failure. Significant fixed effects (p<0.10) are denoted in bold. Random effects are variance and respective 95% credible intervals.

	failure at egg stage				**failure at nestling stage**				**overall nest failure**			
	OR	**95% C.I.**		**p**	**OR**	**95% C.I.**		**p**	**OR**	**95% C.I.**		**p**
		lower	**upper**			**lower**	**upper**			**lower**	**upper**	
fixed effects												
intercept	0.07	0.01	2.14	0.01	**0.01**	**0.00**	**0.05**	**<0.01**	**0.07**	**0.02**	**0.36**	**<0.01**
treatment (predator)[1]	0.74	0.25	2.18	0.59	**3.74**	**1.15**	**12.43**	**0.01**	**2.20**	**1.07**	**5.37**	**0.06**
life history pace	1.36	0.61	2.94	0.40	0.53	0.18	1.40	0.19	0.77	0.39	1.35	0.36
time post-fledging	0.84	0.36	2.08	0.67	0.98	0.45	2.08	0.95	0.84	0.50	1.40	0.51
number of clutches	**2.34**	**0.93**	**6.23**	**0.08**	1.27	0.41	5.16	0.67	1.51	0.69	3.29	0.28
predation risk	0.99	0.95	1.03	0.53	**1.08**	**1.05**	**1.12**	**<0.01**	**1.06**	**1.02**	**1.09**	**<0.01**
nest type (open)[1]	0.30	0.06	1.42	0.12	2.10	0.42	9.58	0.34	1.52	0.54	4.53	0.44
laying date	1.02	0.97	1.06	0.42	0.98	0.92	1.04	0.57	1.01	0.97	1.04	0.67
predator (mammalian)[1]	1.28	0.21	7.77	0.77	0.54	0.10	3.03	0.48	0.91	0.29	3.32	0.87
proximity to nest	1.30	0.57	2.53	0.50	1.01	0.52	1.97	0.96	1.08	0.67	1.75	0.73
treatment (predator) x nest type (open)	**6.82**	**0.89**	**48.42**	**0.03**								
random effects												
Species	0.18	0.0003	0.65		0.30	0.0003	1.22		0.08	0.0002	0.35	
Year	0.25	0.0002	1.10		8.06	0.0003	25.33		0.16	0.0002	0.89	

[1] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an odds ratio (OR) of 1.

Table S3. Correlation matrix, standardized principal components loadings, and communality (h^2) of continuous species traits excluding Siberian jays. Eigenvalues and cumulative variance explained by each component is given.

correlation matrix					**loadings**		**h^2**
	body mass	time in nest	time post-fledging	adult survival	PC1	PC2	
body mass	1	0.59	-0.46	0.95	**0.93**	-0.26	0.99
time in nest (laying – fledging)	0.59	1	0.14	0.52	**0.84**	0.49	0.84
time post-fledging	-0.46	0.14	1	-0.28	-0.14	**0.93**	0.92
adult survival	0.95	0.52	-0.28	1	**0.91**	-0.15	0.89
eigenvalue					2.43	1.21	
cumulative variance explained (%)					0.61	0.91	

Table S4. Model estimates and corresponding standard errors and p-values for predictors of allocation into eggs, excluding Siberian jays. Significant fixed effects (p<0.10) are denoted in bold. Random effects are standard deviation. est.=estimate, p=p-value.

	egg volume			**clutch volume**			**egg volume variation**		
fixed effects	est.	SE	p	est.	SE	p	est.	SE	p
intercept	0.07	0.16	0.66	-0.002	0.29	0.99	-0.10	0.19	0.62
treatment (predator)[1]	0.003	0.02	0.87	**-0.06**	**0.03**	**0.03**	**0.25**	**0.15**	**0.09**
life-history pace	**0.81**	**0.16**	**<0.01**	**1.13**	**0.34**	**0.03**	0.01	0.21	0.95
time post-fledging	-0.23	0.16	0.21	0.27	0.53	0.65	-0.05	0.22	0.83
number of clutches	**0.27**	**0.11**	**0.08**	0.63	0.34	0.13	-0.23	0.21	0.33
predation risk	0.06	0.05	0.30	-0.03	0.07	0.76	0.12	0.18	0.62
nest type (open)[1]	-0.001	0.30	0.99	-0.54	0.70	0.50	-0.44	0.41	0.34
laying date	**-0.02**	**0.01**	**0.07**	**-0.07**	**0.02**	**<0.01**	-0.09	0.09	0.32
predator type (mammalian)[1]	-0.02	0.41	0.96	0.57	0.66	0.45	-0.42	0.55	0.49
proximity to nest	0.05	0.04	0.26	0.01	0.02	0.64	**-0.30**	**0.10**	**<0.01**
clutch size	0.02	0.02	0.16	**0.34**	**0.02**	**<0.01**	0.07	0.12	0.54
treatment (predator)[1] x number of clutches				**-0.06**	**0.03**	**0.03**			
treatment (predator)[1] x time post-fledging							**0.49**	**0.17**	**<0.01**
random effects									
species	0.41			0.75			0.43		
year	<0.01			<0.01			<0.01		
nest	0.10								

[1] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an estimate of 0.

Table S5. Model estimates and corresponding standard errors and p-values for predictors of the number of offspring at each nest stage excluding Siberian jays. Significant fixed effects (p<0.10) are denoted in bold. Random effects are standard deviation. est. =estimate, p=p-value.

	clutch size			**number of nestlings**			**number of fledglings**		
fixed effects	**est.**	**SE**	**p**	**est.**	**SE**	**p**	**est.**	**SE**	**p**
intercept	**1.69**	**0.06**	**<0.01**	**1.42**	**0.06**	**<0.01**	**1.31**	**0.08**	**<0.01**
treatment (predator)[1]	-0.04	0.07	0.61	0.06	0.09	0.46	0.13	0.12	0.28
life-history pace	**-0.13**	**0.06**	**0.04**	0.04	0.04	0.31	0.07	0.05	0.15
time post-fledging	-0.05	0.07	0.41	0.04	0.06	0.44	0.05	0.07	0.50
number of clutches	**-0.22**	**0.06**	**<0.01**	-0.07	0.06	0.20	-0.12	0.08	0.12
predation risk	**0.15**	**0.07**	**0.02**	<0.01	0.05	0.98	0.05	0.08	0.58
nest type (open)[1]	**-0.35**	**0.12**	**<0.01**	0.03	0.10	0.79	0.13	0.17	0.45
laying date	-0.01	0.04	0.73	-0.03	0.05	0.59	-0.01	0.06	0.90
predator type (mammalian)[1]	-0.08	0.10	0.41	0.02	0.10	0.86	<0.01	0.13	0.96
proximity to nest	<0.01	0.05	0.99	-0.05	0.05	0.29	<0.01	0.06	0.99
clutch size	na	na	na	**0.35**	**0.05**	**<0.01**	**0.20**	**0.07**	**<0.01**
random effects									
species	<0.01			<0.01			<0.01		
year	<0.01			<0.01			<0.01		

[1] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an estimate of 0.

Table S6. Odds ratios (OR) and corresponding 95% credible intervals (C.I.) and p-values (p) for predictors of nest failure at the egg stage, nestling stage, and overall nest failure, excluding Siberian jays. Significant fixed effects (p<0.10) are denoted in bold. Random effects are variance and respective 95% credible intervals.

	failure at egg stage				**failure at nestling stage**				**overall nest failure**			
	OR	**95% C.I.**		**p**	**OR**	**95% C.I.**		**p**	**OR**	**95% C.I.**		**p**
		lower	**upper**			**lower**	**upper**			**lower**	**upper**	
fixed effects												
intercept	0.66	0.16	2.27	0.55	**0.13**	**0.04**	**0.33**	**<0.01**	0.61	0.31	1.16	0.14
treatment (predator)[1]	0.77	0.28	2.32	0.64	**3.56**	**1.19**	**13.60**	**0.03**	**1.99**	**0.90**	**5.10**	**0.09**
life history pace	0.73	0.37	1.54	0.31	0.53	0.18	1.62	0.23	0.76	0.41	1.40	0.32
time post-fledging	0.93	0.34	2.29	0.88	0.64	0.19	1.97	0.40	0.84	0.43	1.67	0.59
number of clutches	**0.96**	**0.91**	**1.01**	**0.09**	1.48	0.54	4.14	0.36	1.32	0.73	2.44	0.34
predation risk	1.79	0.61	5.53	0.25	**4.66**	**2.44**	**10.49**	**<0.01**	**2.69**	**1.42**	**4.90**	**<0.01**
nest type (open)[1]	0.59	0.09	3.71	0.59	2.12	0.26	21.76	0.47	2.27	0.58	8.85	0.19
laying date	1.02	0.99	1.06	0.26	0.73	0.30	1.60	0.47	1.06	0.66	1.63	0.81
predator (mammalian)[1]	1.54	0.27	8.00	0.50	0.60	0.09	4.90	0.60	0.88	0.24	3.35	0.83
proximity to nest	3.74	0.68	21.76	0.14	0.76	0.41	1.39	0.40	0.80	0.20	3.86	0.77
treatment (predator) x nest type (open)	**19.89**	**2.29**	**202.35**	**<0.01**								
random effects												
species	0.32	0.001	1.14		0.39	0.002	1.70		0.19	0.002	0.71	
year	1.66	0.002	6.09		25.8	0.004	85.44		0.66	0.002	1.75	

[1] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an odds ratio (OR) of 1.

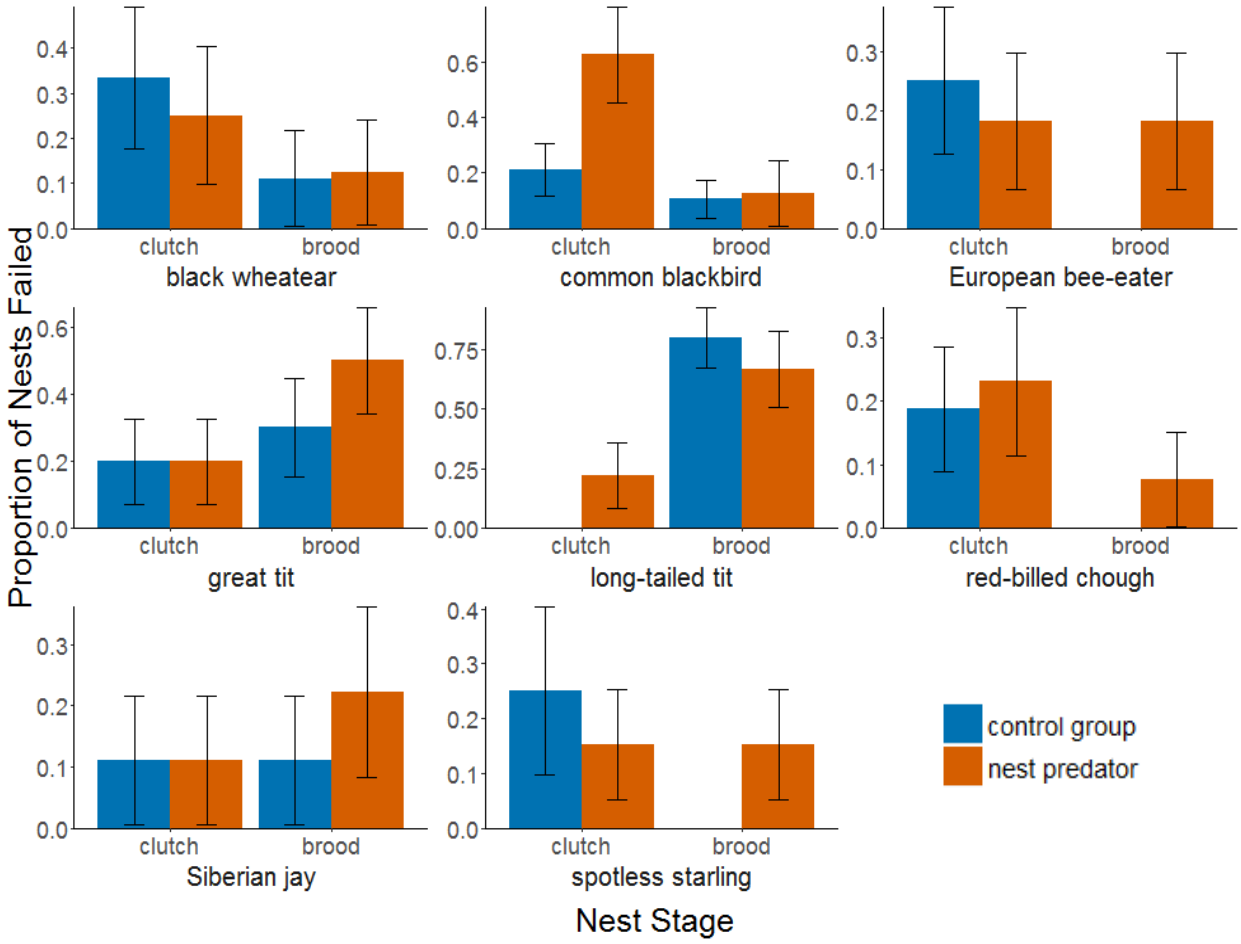

Figure S1. Nest failures (proportion failed +/- SE) at the egg stage and the nestling stage per treatment.

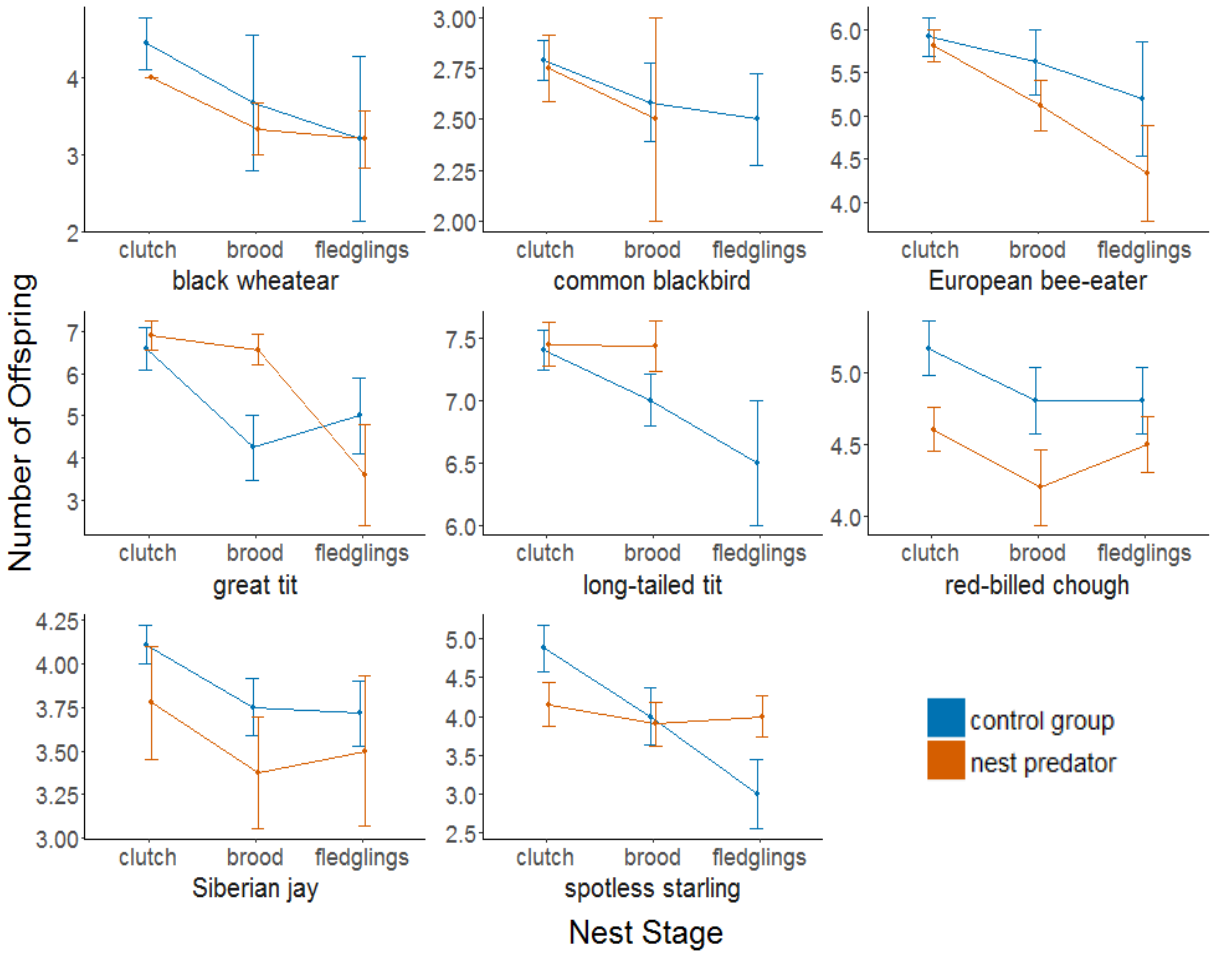

Figure S2. The number of eggs, nestlings and fledglings per treatment for each species, including only the nests that succeeded in the respective phase.

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Experimentally increased costs of parental care are shunted to offspring in species with extended care

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Abstract

Biparental care systems are a valuable model to examine conflict and cooperation between unrelated individuals, as the reproductive decisions of each parent determine their own fitness. A common experimental technique for testing responses to changes in the costs of parental care is to temporarily handicap one parent, inducing a higher cost of providing care. However, dissimilarity in experimental designs of these studies has hindered interspecific comparisons of the patterns of cost distribution between parents and offspring. Here we apply a comparative experimental approach by handicapping parents of five bird species using the same experimental treatment. In some species, a decrease in care by a handicapped parent was compensated by its partner, while in others the increased costs of care were shunted to the offspring. Parental responses to an increased cost of care primarily depended on the total duration of care that offspring require. However, life history pace (i.e., adult survival and fecundity) did not influence parental decisions when faced with a higher cost of caring. Our study highlights that a greater attention to intergenerational trade-offs is warranted, particularly in species with a large burden of parental care. Moreover, we demonstrate that parental care decisions may be weighed more against physiological workload constraints than against future prospects of reproduction, supporting evidence that avian species may devote comparable amounts of energy into survival, regardless of life history strategy.

Introduction

Parental care is widespread in animals, but its expression varies greatly among and within species (Cockburn 2006, Royle et al. 2012) as well as within individuals (Eggers et al. 2008, Ghalambor et al. 2013, Caro et al. 2016). Biparental care is a particularly interesting system of parental care, as the product of the interactions between the parents is vital to the fitness of both individuals. Birds are unique among the taxonomic classes in regard to the prevalence of biparental care: both parents contribute care to the offspring in an estimated 90% of bird species (Cockburn 2006), while in other clades biparental care is much rarer (percentage of genera with bi-parental care: teleost fish: 3%, anurans: 1%, mammals: 9%, squamate reptiles: 0%, Gross and Sargent 1985; insects: 22% of species with any parental care, Suzuki 2013).

Biparental care relies on cooperation between parents to ensure the survival of their offspring, but is also a source of conflict. Both parents face a trade-off between current and future reproduction and should strive to reduce their own effort, in balance with their partner's effort, to ensure that offspring receive enough total care to survive while lessening current costs of parental care for themselves (Trivers 1972, Drent and Daan 1980). A pioneering model suggested that investment in parental care of both parents can be an evolutionary stable strategy (ESS) if one parent reduces its effort, its partner partially compensates and the increased costs are distributed between the partner and the offspring (Houston and Davies 1985). Recent models have predicted that negotiation between the parents could lead to partial, full or no compensation by partners, depending on the costs and benefits associated with care (Jones et al. 2002, Johnstone and Hinde 2006). This negotiation process has been suggested to be influenced by several species traits, such as brood size, developmental mode and lifespan (Silver et al. 1985, Kokko and Jennions 2003, Olson et al. 2008), however experimental tests of these ideas are lacking.

Table 1. Results from previous studies that increased the costs of parental care through feather removal.

Species	Condition			Care Behavior		Reference
	Focal	Partner	Offspring	Focal	Partner	
blue tit *Cyanistes caeruleus*	-	-	≈	-	≈	(Slagsvold and Lifjeld 1990)
coal tit *Parus ater*	-					(Slagsvold and Lifjeld 1990)
great tit *Parus major*	-	≈	-			(Slagsvold and Lifjeld 1990)
tree swallow *Tuchycineta bicolor*			≈	≈	+	(Whittingham et al. 1994)
Leach's storm-petrel *Oceanodroma leucorhoa*	≈		-	-		(Mauck and Grubb Jr 1995)
thin-billed prion *Pachyptila belcheri*	-		≈			(Weimerskirch et al. 1995)
tree swallow *Tuchycineta bicolor*	-			-		(Winkler and Allen 1995)
pied flycatcher *Ficedula hypoleuca*	≈	≈	-	≈	≈	(Moreno et al. 1999)
great tit *Parus major*	≈	≈	≈	-	+	(Sanz et al. 2000)
blue-footed boobie *Sula nebouxii*	-		-			(Velando 2002)
blue-footed boobie *Sula nebouxii*	≈	-	-			(Velando and Alonso-Alvarez 2003)
common tern *Sterna hirundo*	-		+			(Nisbet et al. 2004)
Cory's shearwater *Calonectris diomedea*	≈		-	-		(Navarro and González-Solís 2007)
cape gannet *Morus capensis*	-	≈	-	-	+	(Bijleveld and Mullers 2009)
little auk *Alle alle*	-	-	-			(Harding et al. 2009)
black-legged kittiwake *Rissa tridactyla*	-	≈	≈	≈	-	(Leclaire et al. 2011)
thick-billed murre *Uria lomvia*	≈		-			(Jacobs et al. 2013)
great tit *Parus major*	-		-	-		(Wegmann et al. 2015)

A common experimental technique for testing changes in the costs of parental care is to temporarily handicap one parent, thereby increasing the cost of providing care. In birds, this is often accomplished through the removal of flight feathers. These handicapping experiments have demonstrated large between-species variation in responses to changes in one parent's physical condition, across both parents and their offspring (Table 1). Handicapped birds may maintain or reduce their physical condition and/or their parental effort. Non-experimental individuals may fully compensate their partner's decrease in care, partially compensate, or copy the behavior of their partner (i.e., decrease care if their partner decreases care). Similarly, the condition of offspring may improve, decline, or stay constant. Although there have been many experimental manipulations of parental care, to our knowledge only one meta-analysis has previously examined the responses comparatively (Harrison et al. 2009). However, due to variation in the types of manipulation (e.g. clipping feathers vs. adding weight), the behavior examined (e.g., feeding vs. incubation) and the types of responses recorded (e.g., parental behavior vs. parental condition), a thorough examination of the mitigating factors for patterns of parental care across species has not been possible. Indeed, this meta-analysis showed that the type of manipulation played a key role in explaining heterogeneity in parental responses to manipulation of care and that responses differed depending on the behavior being focused on, while species traits that may have accounted for interspecific differences were largely excluded from the analyses.

A drawback of many handicapping studies is that they measure effects on a single trait or individual, by focusing only on the condition or behavioral changes of the handicapped parent, its partner or their offspring (see Table 1). Consequently, it is difficult to determine how experimental effects are distributed between parents and offspring in many cases. Furthermore, the most common measure taken has been changes in the condition of the handicapped individual (Table 1), usually in terms of body mass, which are frequently attributed to an increased reproductive effort. However, these responses may reflect functional corrections to wing loading rather than adverse effects of

handicapping (Norberg 1981, Lind and Jakobsson 2001), confounding whether there are any changes in reproductive effort. Because changes in the body mass of handicapped birds are difficult to interpret, it is important to measure parental effort directly, via behavioral responses, in combination with the condition of the offspring, so that relative effects can be properly estimated across all of the family members.

Here we handicapped parents in five bird species with bi-parental care, resulting in one partner facing higher costs of offspring provisioning, which must be paid by the treated bird, its partner, or their offspring. We analyzed the results comparatively to examine differences in parental care behavior of each parent and any effects on nestling condition. Life-history theory predicts that long-lived species should prioritize survival (and thus future reproduction) over current reproduction, and they are consequently expected to be less willing to increase their parental effort compared to short-lived species (Williams 1966, Drent and Daan 1980). However, a more recent comparative analysis on costs of care suggests that all individuals may allocate the same amount of energy to survival, regardless of their life-history pace (Santos and Nakagawa 2012). Thus, we expected that responses will vary across a life-history spectrum, but that life history pace alone will not account for interspecific differences.

Methods

STUDY SPECIES

We handicapped individuals of five bird species with biparental care in southern Spain during the breeding seasons of 2013 and 2014. The experiment was conducted in populations of great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), and woodchat shrikes (*Lanius senator*) in the Cordoba region (37°95’N, 4°40'W), and black wheatears (*Oenanthe leucura*) and European bee-eaters (*Merops apiaster*) in the Guadix region (37°25’N, 3°05’W). All nests used in the analyses had two adults, presumably the mother and father, attending to the nestlings. At least one parent was marked for

individual identification prior to the experiment, with a combination of plastic colored rings or a temporary mark on their feathers. Because European bee-eaters sometimes have helpers at the nest, both parents were marked early in the nest stages (building or incubating) to reduce the chances of marking a non-breeder, and each nest included in this study was checked for the presence of only 2 adults attending the nest at the time of the experiment.

EXPERIMENTAL DESIGN

Experiments were started at each nest based on the developmental stage of the nestlings (as feather growth begins), rather than absolute age, to allow for a better comparison between species with different development schedules. The experimental procedure spanned five days. Each nest was recorded with a video camera to obtain the feeding rate for 2-4 hours on the first, second, fourth and fifth days of the experiment. The duration of recording was determined prior to the experiment through observations of each species, and was based on the natural feeding rate to conservatively ensure a minimum of ten feeding visits per observational bout. Recordings were made at the same time for each nest, and nests were assigned to morning, midday or afternoon recordings using a balanced random design.

On the third day of the experiment one of the adults at each nest was caught and either handicapped, by removing the 7th and 9th primary feathers on each wing, or was handled (with simulated feather removal) and released as a control. Removal of flight feathers has been demonstrated to increase the energetic demands of flight by increasing wing loading (Pennycuick 1989, Hedenström and Sunada 1999), thus increasing the cost of parental care during foraging for provisioning.

After recording on the first day, all nestlings were marked for individual identification with a non-toxic permanent marker on one leg. Each nestling was weighed with a digital scale and its wing and tarsus length were measured with dial calipers (0.1mm accuracy) on the first, third and fifth day

of the experiment. All nestling measurements within a nest were taken by the same experimenter to maintain consistency across days.

STATISTICAL ANALYSES

We predicted that the visitation rates of parents after one parent is handicapped may be influenced by the adult survival rate, body mass, the body mass–scaled initial reproductive allocation (total mass of eggs produced annually divided by adult body mass, following Sibly et al. 2012), the duration that offspring require provisioning, and the duration that offspring stay with their parents subsequent to nutritional independence. We used a principal component analysis (PCA) to reduce the dimensionality of these predictors, as most of them exhibited moderate to strong correlations (Table S1). Because the units of measurement for traits differed, we relied on the correlation matrix among variables to generate PCA scores rather than the covariance matrix (Graham 2003). Both the inspection of a Scree plot and Eigenvalues suggested the extraction of 2 principal components (PCs). To simplify the factor structure by maximizing the variances of loadings and hence facilitate their interpretation, we first performed an oblique (oblimin) rotation of the components, which indicated that the resulting factors were not substantially correlated (r=0.21). We then applied a varimax rotation to the original components. Differences in results of the rotation techniques were negligible, and did not affect the overall pattern of loadings, so we retained the varimax rotation in further analyses (Kieffer 1998).

The principal components analysis resulted in the extraction of two PC variables (Table S1) which cumulatively explained 79% of the variance. The first component, hereafter labelled “duration of care”, included the number of days that offspring are provisioned by their parents (‘care time’), body mass, and the number of days that offspring stay with their parents post-nutritional independence ('family time', Drobniak et al. 2015). A high value of this component signifies species with long periods of parental care. The second component, hereafter labelled “life history pace”,

included adult survival rate and the index of reproductive allocation (see above). A high value of this component signifies parents with long expected lifespans and low annual reproductive investment.

We fit linear mixed models using a Bayesian framework with Markov chain Monte Carlo (MCMC) methods with the package MCMCglmm (Hadfield 2010) in R 3.1.0 (R Core Team 2014) to examine among-species responses to the handicapping procedure. All models were run for 100'000 iterations, with a burn-in phase of 2'000 iterations and a thinning interval of 100, which resulted in approximately 1'000 samples from the posterior distributions for each model parameter. A reasonably normal distribution of residuals was confirmed for all models. Model convergence was confirmed by visual examination of trace plots and calculation of autocorrelation between iterations. Because initial models included several 2- and 3-way interactions (see below), non-significant interactions ($p>0.05$) were removed from initial models using a backwards elimination procedure, except for the interaction between treatment and phase. The interaction between treatment and phase was expected a priori and is the main result of our experiment, as we only expect an experimental effect during the post-treatment phase. Results of all initial models, prior to removal of any non-significant terms, are included in the Supplementary Material, to facilitate comparison of models and effect sizes for both significant and non-significant factors.

Visitation rates

Visitation rates were measured as the number of nest visits per hour per nestling. Although we did not confirm that every visit involved food delivery, visitation during the nestling phase is a common proxy for offspring provisioning (Mariette et al. 2011, Mutzel et al. 2013). These rates were averaged for experimental days 1 and 2, i.e, 'pre-treatment' phase, and experimental days 4 and 5, i.e., 'post-treatment' phase. We first analyzed sources of variation in visitation rates among the tested species using linear mixed-effect models with the total feeding rate at the nest as the response variable. Brood size, duration of care, life history pace, phase, and treatment were included as fixed effects, with

random intercepts for species and nest identity. Because of the experimental design, changes in chick provisioning after the treatment could potentially be confounded by an effect of time, if feeding rates naturally change over the nesting period. Therefore, treatment effects were also examined by including three-way interactions, and their contained two-way interactions, of phase and treatment with each principal component. Non-significant main effects were retained in the final model while non-significant interactions were removed from final models, except for the interaction between treatment and phase.

Our analyses revealed a significant 3-way interaction between phase, treatment and duration of care for the total visitation rate (see Results). To interpret this interaction, we carried out two additional models, examining treatment effects in the pre-treatment phase and the post-treatment phase separately. These models included brood size, duration of care, life history pace, and the two-way interaction between duration of care and treatment as fixed effects, with species as a random factor.

We then examined treatment effects on the feeding rates of the focal individuals (i.e. handicapped or control-caught). We included brood size and separate three-way interactions between treatment, phase, and each principal component (and their contained two-way interactions and main effects) as fixed effects, with species and nest identity as random factors. Non-significant interactions were sequentially removed from final models, but non-significant main effects were retained. Because we found no significant 3-way interactions in this model, no additional models were run.

Nestling Growth

We analyzed sources of variation in nestling growth among all of the tested species using separate linear mixed-effect models of nestling changes in mass, tarsus length, and wing length. Each response variable was measured as the difference in each parameter between the pre-treatment phase (days

1-2), and the difference in each measurement of the post-treatment phase (days 4-5). Brood size, duration of care, life history pace, phase, and treatment were included as fixed effects. Random intercepts were specified for species, nest identity, nestling identity (unique combinations of nest identity and nestling number), and nest phase (unique combinations of nest identity and phase). Changes in chick growth after the treatment could potentially be confounded by an effect of time, if growth rates naturally change over the nesting period. Therefore, treatment effects were examined by including three-way interactions, and their contained two-way interactions, of phase, treatment and each principal component. Because a significant interaction between phase and treatment was expected a priori, this interaction was maintained in all models regardless of significance. All other non-significant interactions were removed from final models, but non-significant main effects were retained.

Our analyses revealed a significant 3-way interaction between phase, treatment and duration of care for changes in nestling body mass (see Results). To interpret this interaction, we carried out 2 additional models, examining the treatment effects of nestling mass change separately in the pre-treatment phase and the post-treatment phase. These models included brood size, adult survival rate, and the two-way interaction between duration of care and treatment as fixed effects, with species as a random factor.

Results

VISITATION RATES

Results of visitation rates (visits per hour and nestling) are based on 72 nests (Table 2). Independent of the treatment, a long duration of care was related to higher individual parental visitation rates (Table 3) and marginally related to higher total visitation rates (Table 4). Neither the brood size nor life history pace were related to individual (Table 3) or total (Table 4) visitation rates. The visitation rate of focal individuals did not change between experimental phases in control nests, while focal

parents reduced their visits after being handicapped (Table 3, Fig. 1). Although the individual rates were significantly lower in the handicapped group, this effect did not interact with any other explanatory variables.

Table 2. Sample sizes of nests and nestlings for each species.

common name	scientific name	treatment n		control n	
		nests	nestlings	nests	nestlings
Blue tit	*Cyanistes caeruleus*	6	44	7	52
Black wheatear	*Oenanthe leucura*	8	28	7	25
European bee-eater	*Merops apiaster*	8	39	7	28
Great tit	*Parus major*	7	52	7	51
Woodchat shrike	*Lanius senator*	7	26	8	38

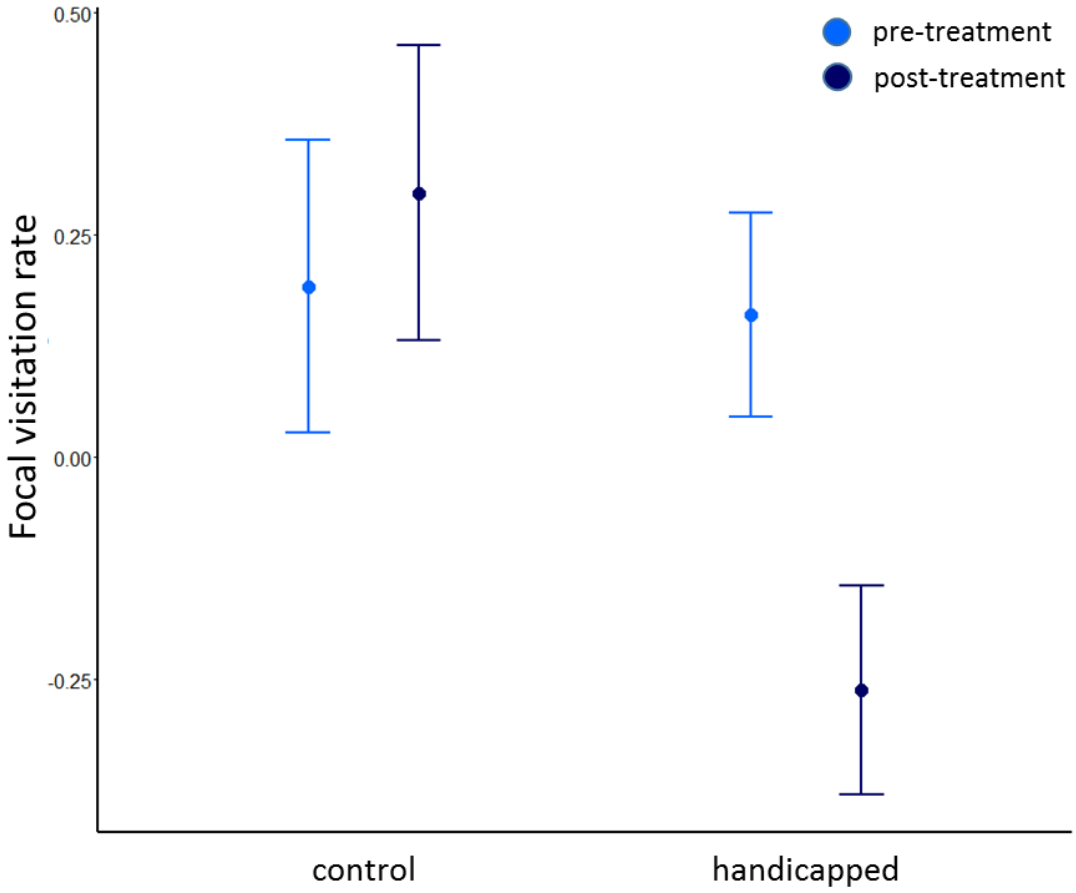

Figure 1. Standardized predicted values (+/- SE) from mixed model of focal bird per-nestling visitation rates. Prior to the treatment, visitation rates did not differ between the control group and treatment group. After the treatment, handicapped birds reduced their visitation rate.

Table 3. Selected mixed model results of effects on focal individual visitation rate. Significant effects (p<0.05) are denoted in bold. Full model results are presented in Table S2.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.350	-0.310	0.842	0.151
duration of care	**1.059**	**0.509**	**1.560**	**0.016**
life history pace	0.341	-0.092	0.829	0.120
brood size	0.266	-0.224	0.693	0.325
pre-treatment phase	-0.140	-0.539	0.230	0.471
treatment	**-0.619**	**-1.021**	**-0.245**	**<0.001**
treatment x pre-treatment phase	**0.535**	**0.032**	**1.072**	**0.047**
random effects				
species	0.295	<0.001	1.361	
nest	0.006	<0.001	0.051	

Total visitation rates were significantly affected by a 3-way interaction between treatment, phase and duration of care (Table 4). Post-hoc examination of this relationship revealed that there was no difference between the pre-treatment phase of the control and the handicapped groups in total visitation rate (estimate= -0.13 95%CI= -0.40, 0.16, p=0.36; Fig. 2A), nor any effects of any of the explanatory variables (Table A4). In contrast, the total visitation rates in the post-treatment phase were lower in handicapped individuals than control individuals (estimate= -0.46, 95%CI=-0.81,-0.12, p=0.008, Table S5). Duration of care interacted with the treatment, indicating that the experimental effect was strongest in species with long parental care periods (estimate= -0.35, 95%CI=-0.70, -0.03; p=0.040; Fig. 2B).

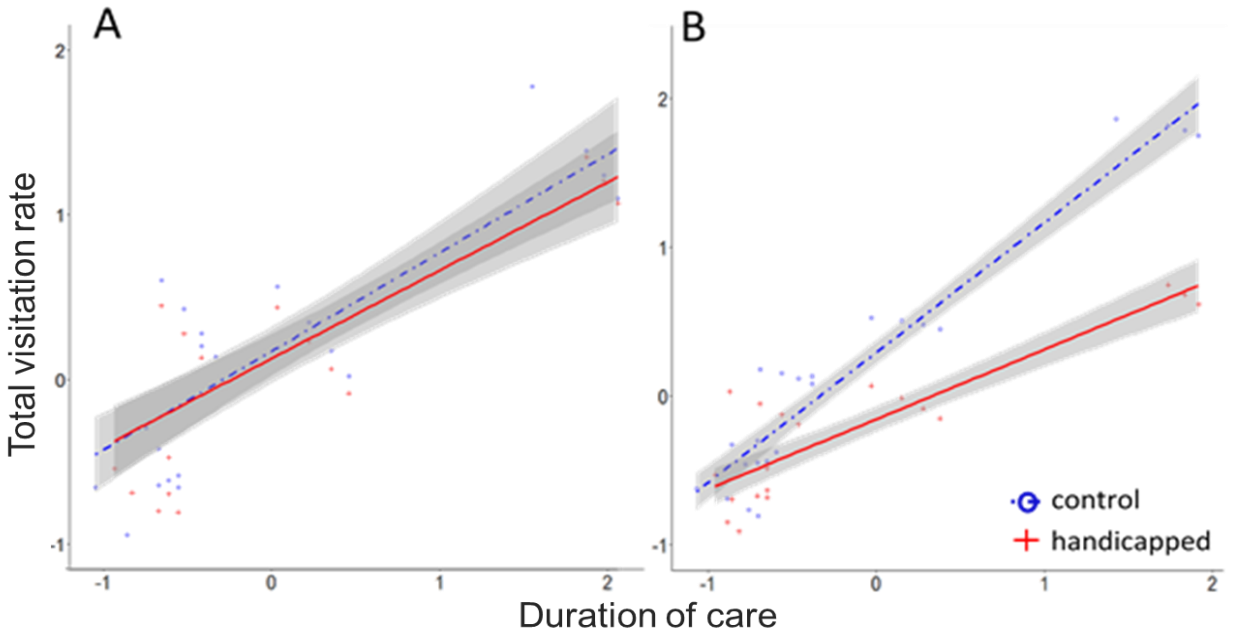

Figure 2. Standardized model-predicted total visitation rates varied according to duration of care. **(A)** Handicapped and control groups had similar visitation rates during the pre-treatment phase **(B)** Total visitation rates were lower in the handicapped group during the post-treatment phase, particularly for species with long durations of care. Shaded area represents 95% confidence interval.

Table 4. Selected mixed model results of effects on total visitation rate at the nest. Significant effects ($p<0.05$) are denoted in bold. Full model results are presented in Table S3.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.217	-0.540	0.887	0.443
duration of care	0.699	-0.129	1.411	0.065
life history pace	0.315	-0.096	0.737	0.120
brood size	-0.094	-0.326	0.168	0.444
pre-treatment phase	-0.100	-0.319	0.075	0.310
treatment	**-0.424**	**-0.711**	**-0.162**	**0.006**
treatment x pre-treatment phase	**0.312**	**0.055**	**0.564**	**0.016**
duration of care x pre-treatment phase	0.076	-0.163	0.294	0.495
duration of care x treatment	-0.287	-0.601	0.006	0.053
duration of care x pre-treatment phase x treatment	**0.334**	**0.050**	**0.613**	**0.020**
random effects				
species	0.785	<0.001	2.642	
nest	0.186	0.087	0.291	

NESTLING GROWTH

Nestling growth data was based on 384 nestlings (Table 2). Changes in nestling mass (Table 5) mirrored the results of total visitation rates and was influenced by a 3-way interaction between duration of care, phase, and treatment. The change in nestling mass did not differ in the pre-treatment phase according to any of our explanatory variables (Fig. 3A, Table S7). In the post-treatment phase (Table S8), the change in body mass of nestlings in the handicapped group decreased with an increasing duration of care, while the mass change of nestlings in the control group increased with an increasing duration of care (Fig. 3B). Changes in nestling mass also depended on life history pace, independent of the treatment, but was not related to any other explanatory variable.

Table 5. Selected mixed model results of changes in nestling mass. Significant effects ($p<0.05$) are denoted in bold. Full model results are presented in Table S6.

Effects	**Estimate (β)**	**95% CI lower**	**upper**	**pMCMC**
fixed effects				
intercept	0.167	-0.120	0.460	0.233
duration of care	0.050	-0.218	0.315	0.724
life history pace	**0.227**	**0.035**	**0.412**	**0.036**
brood size	0.030	-0.181	0.222	0.779
pre-treatment phase	-0.175	-0.433	0.099	0.234
treatment	-0.309	-0.682	0.075	0.108
treatment x pre-treatment phase	0.309	-0.073	0.680	0.122
duration of care x pre-treatment phase	0.138	-0.135	0.412	0.330
duration of care x treatment	-0.345	-0.688	0.019	0.057
duration of care x pre-treatment phase x treatment	**0.429**	**0.017**	**0.776**	**0.026**
random effects				
species	0.003	<0.001	0.010	
nest	0.281	0.132	0.474	
nestling	0.001	<0.001	0.007	
nest phase	0.238	0.131	0.374	

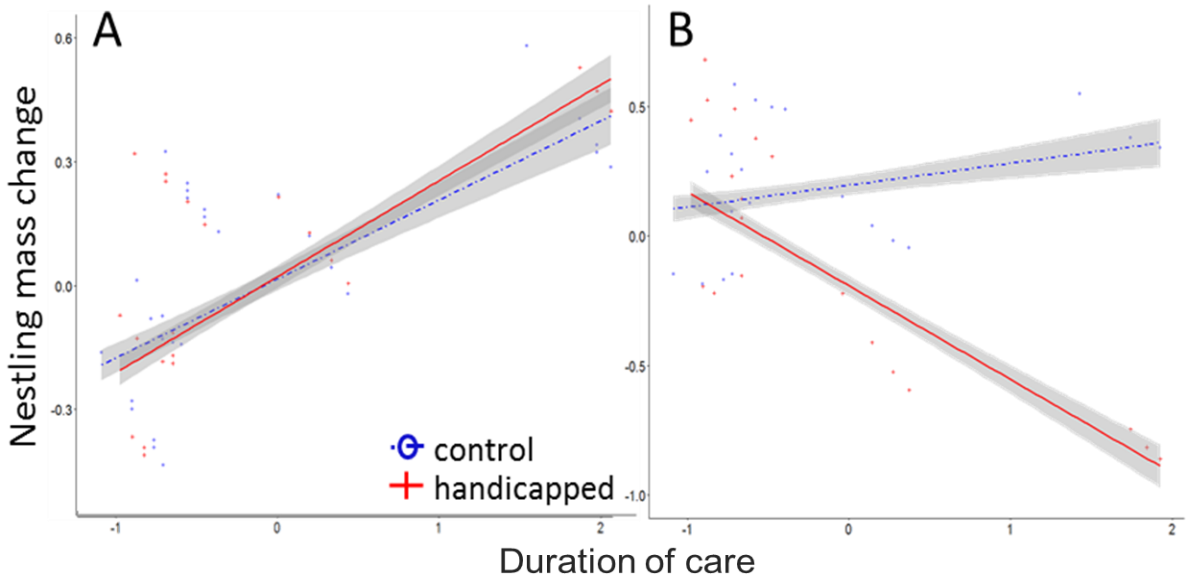

Figure 3. Standardized model-predicted changes in nestling mass varied according to duration of care: (A) The change in nestling mass did not differ between the handicapped and control groups in the pre-treatment phase (B) In the post-treatment phase, the mass of nestlings in the handicapped group decreased with an increasing duration of care, while the mass of nestlings in the control group increased with the duration of care. Shaded area represents 95% confidence interval.

Analyses of changes in nestling tarsus and wing growth (detailed in Tables S9-S12) indicated no treatment effects on either response variable. Both wing and tarsus growth changed over time, irrespective of treatment group, with nestlings having larger tarsus growth in the pre-treatment phase (estimate=0.59, 95%CI=0.26, 0.94, p<0.001), and larger wing growth during the post-treatment phase (estimate=-0.39, 95%CI=-0.78,-0.05, p=0.042). Tarsus growth also significantly decreased with an increasing duration of care (estimate=-0.58, 95%CI=-0.76,-0.43, p=0.004), independent of the treatment.

Discussion

Parental care is costly, and parents of iteroparous species are predicted to strive to minimize the costs that they incur in a current reproductive event to ensure future reproductive events (Williams 1966, Stearns 1992, Gross 2005). Our experiments demonstrate that, across 5 species, an increased cost of parental care generally results in a reduced visitation rate by the manipulated parent, and that the

additional costs are shared by its partner and their offspring. The strength of this effect was mediated by the duration of care that the offspring require; in large species with long care periods, the offspring were passed the largest share of the additional cost, while the partner increased their effort more in species with relatively short parental care periods. This result was evident in both changes to nest visitation rates of the parents and the body mass gain of the offspring.

Given the limited number of samples and species in this study, it faced several limitations. Responses may have varied according to factors we were unable to include due to a lack of statistical power and a lack of variation within the species included here. In particular, the scope of this study did not allow for examination of ecological factors; environmental unpredictability and a species' niche are likely to affect parental care decisions in ways that we were unable to test. For example, European bee-eaters are the only specialized aerial foragers among the species we tested, and consequently handicapped individuals may have accrued higher costs of foraging, particularly because gaps in flight feathers reduce flight maneuverability (Swaddle and Witter 1997). However, among the species included here, we only found differences in the compensatory behavior of partners rather than in the reduction of care by handicapped individuals. Thus, the effects of the handicapping treatment *per se* appeared to similarly influence the species included in this study. Moreover, it is possible that parents altered the quality or quantity of the food that they delivered to the nestlings, rather than the number of visits (Wright et al. 1998). Yet, changes in the condition of the nestlings matched the changes to total provisioning rates at the nest, indicating that costs were in fact accrued by nestlings with a handicapped parent. The findings of this study give novel empirical insight into the different strategies employed across species to deal with increased costs of parental care, but should be verified with larger-scale comparative studies. Such studies will be made possible with targeted experimental tests that manipulate parental care in a standardized way, so that comparable effect sizes are obtainable.

Little is known about the physiological effects of workload during parental care in free-living birds (Williams and Fowler 2015), but previous studies suggest that costs of parental care can be cumulative over a breeding cycle. Many bird species have been shown to rely (at least partially) on nutrient reserves built-up prior to breeding and/or during incubation (Drent and Daan 1980, Martin 1987, Moreno 1989), in preparation for the costly provisioning stage of parenting. Thus, the workload during provisioning may be at or higher than the maximum sustainable workload (Weiner 1992, Low et al. 2012). If the maximum sustainable workload is exceeded over a long period, the risk of mortality is expected to increase (Drent and Daan 1980). Accordingly, parents are predicted to make decisions about parental care based on maintaining their physical condition above a threshold determined by the trade-off between offspring survival and their expected reproductive value at the end of breeding (Webb et al. 2002). Indeed, theory demonstrates that an increase in the daily energetic costs of care leads to a decrease in the duration of care in birds (Webb et al. 2002), and field data shows that species with long provisioning periods often have a greater loss of body mass than species with short durations of provisioning (Moreno 1989). Moreover, costs associated with extended parental care have been shown to have important carryover effects; for example, geese (*Branta bernicla*) with families in a given season are less likely to breed successfully in the following season (Inger et al. 2010). Taken together, these findings indicate that both the daily energy expenditure and the duration that expenditure must be sustained contribute to the overall costs of parental care.

Across all birds, large-bodied species with long care periods generally have low adult mortality (Speakman 2005, Valcu et al. 2014). However, in the set of species that we investigated, these traits were not highly correlated, thus we were able to tease apart where species lie on the spectrum of the trade-off between survival and reproduction. Here, the species with the largest opportunity for future reproduction differed from those with the longest burden of parental care. We expected that parents with a slow life history would be most sensitive to costs of reproduction (Williams 1966, Drent and Daan 1980, Linden and Møller 1989). However, only the duration of care but not life-history pace

predicted the observed patterns in our study. The latter determined whether costs were passed to offspring while the former did not affect parental care decisions when faced with an increased cost of care. In accordance with our findings, a meta-analysis that looked explicitly at energy expenditure of handicapped birds found that a species' life history was independent of whether individuals reduced investment into their own energy stores or their offspring's growth (Elliott et al. 2014).

Parents with low baseline costs of parental care probably have more leeway to increase their parental behavior without incurring deleterious consequences, and thus costs allocated to offspring can be minimized in these species. In contrast, parents with generally high costs of parental care are more likely to be at their maximum energetic capacity in a given reproductive event, and any increase in the costs associated with caring may have severe consequences in terms of future fitness and survival. Larger species do indeed expend more energy per day toward parental care than small species, however the ratio of energy expenditure to body mass tends to be smaller in large species (Masman et al. 1989). Thus, our results appear contrary to the prediction that large species expend the smallest share of their energy during parental care (Masman et al. 1989). However, this prediction is based on per-day calculations of energy expenditure relative to energy intake, and does not take into account the duration of care, which is generally longer for large species and thus may accrue higher reproductive costs over the whole breeding cycle.

Most studies of the costs of parental care focus on the trade-off between current and future reproduction or survival (intraindividual trade-offs, e.g., Owens and Bennett 1994, Webb et al. 2002, Alonso-Alvarez and Velando 2012, Santos and Nakagawa 2012), while relatively few studies have addressed the fitness consequences of parental decisions on current offspring (intergenerational trade-off, as discussed in Stearns 1989). Our results suggest that greater attention to intergenerational trade-offs is warranted, particularly in large species with long developmental (and thus parental care) periods. Moreover, our results indicate that, across species, parental care decisions may be weighed more against physiological workload constraints than against future prospects of reproduction, and

support recent evidence that all bird species may devote comparable amounts of energy into survival, regardless of life history strategy (Santos and Nakagawa 2012, Elliot et al. 2014).

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Supplementary Material

Table S1. Correlation matrix, standardized principal components loadings, and communality (h2) of continuous species traits. Eigenvalues and cumulative variance explained by each component is given.

correlation matrix						loadings		h^2
	body mass	care time	family time	adult survival	reproductive allocation	PC1	PC2	
body mass	1	0.59	0.83	0.64	-0.28	**0.86**	0.47	0.97
care time	0.59	1	0.49	0.00	-0.16	**0.78**	-0.01	0.61
family time	0.83	0.49	1	0.24	0.10	**0.92**	0.03	0.84
adult survival	0.64	0.00	0.24	1	-0.51	0.20	**0.88**	0.81
reproductive allocation	-0.28	-0.16	0.10	-0.51	1	0.02	**-0.85**	0.73
eigenvalue						2.59	1.38	
cumulative variance explained (%)						0.45	0.79	

Table S2. Full mixed model results of effects on focal individual visitation rate.

Effects	Estimate (β)	95% CI lower	95% CI upper	pMCMC
fixed effects				
intercept	0.209	-0.320	0.672	0.263
duration of care	**0.796**	**0.242**	**1.204**	**0.022**
life history pace	**0.423**	**0.144**	**0.751**	**0.002**
brood size	0.257	-0.099	0.578	0.190
pre-treatment phase	-0.098	-0.476	0.230	0.588
treatment	**-0.465**	**-0.813**	**-0.104**	**0.006**
treatment x pre-treatment phase	0.386	-0.071	0.925	0.112
treatment x duration of care	-0.377	-0.765	-0.009	0.051
treatment x life history pace	0.255	-0.641	0.050	0.149
duration of care x pre-treatment phase	0.310	-0.141	0.709	0.173
life history pace x pre-treatment phase	0.027	-0.324	0.391	0.878
duration of care x pre-treatment phase x treatment	0.249	-0.277	0.788	0.345
life history pace x pre-treatment phase x treatment	0.124	-0.338	0.631	0.629
random effects				
species	0.186	<0.001	0.665	
nest	0.005	<0.001	0.029	

Table S3. Full mixed model results of effects on total visitation rate at the nest.

Effects	Estimate (β)	95% CI lower	95% CI upper	pMCMC
fixed effects				
intercept	0.215	-0.522	1.101	0.434
duration of care	0.704	-0.157	1.412	0.055
life history pace	**0.469**	**0.076**	**0.839**	**0.014**
brood size	-0.077	-0.334	0.165	0.537
pre-treatment phase	-0.106	-0.308	0.085	0.312
treatment	**-0.415**	**-0.712**	**-0.119**	**0.010**
treatment x pre-treatment phase	**0.303**	**0.013**	**0.595**	**0.047**
treatment x duration of care	-0.307	-0.607	0.012	0.069
treatment x life history pace	-0.184	-0.463	0.088	0.204
duration of care x pre-treatment phase	0.077	-0.128	0.296	0.490
life history pace x pre-treatment phase	-0.004	-0.204	0.163	0.929
duration of care x pre-treatment phase x treatment	**0.359**	**0.085**	**0.622**	**0.012**
life history pace x pre-treatment phase x treatment	0.138	-0.126	0.393	0.280
random effects				
species	0.701	<0.001	2.749	
nest	0.188	0.080	0.303	

Table S4. Mixed model results of effects on total visitation rates during pre-treatment phase.

Effects	Estimate (β)	95% CI lower	95% CI upper	pMCMC
fixed effects				
intercept	0.091	-0.705	1.002	0.767
duration of care	0.634	-0.208	1.484	0.108
life history pace	0.375	-0.095	0.845	0.084
brood size	-0.154	-0.457	0.107	0.271
treatment	-0.126	-0.403	0.160	0.363
treatment x duration of care	0.037	-0.237	0.300	0.782
random effects				
species	0.923	<0.001	3.488	

Table S5. Mixed model results of effects on total visitation rates during post-treatment phase.

Effects	Estimate (β)	95% CI lower	95% CI upper	pMCMC
fixed effects				
intercept	0.263	-0.668	1.230	0.394
duration of care	0.829	-0.082	1.597	0.065
life history pace	0.192	-0.393	0.656	0.414
brood size	-0.087	-0.435	0.251	0.675
treatment	**-0.455**	**-0.806**	**-0.122**	**0.008**
treatment x duration of care	**-0.348**	**-0.695**	**-0.025**	**0.040**
random effects				
species	0.741	<0.001	2.751	

Table S6. Full mixed model results of effects on nestling mass gain.

Effects	Estimate (β)	95% CI lower	95% CI upper	pMCMC
fixed effects				
intercept	0.140	-0.111	0.464	0.259
duration of care	0.054	-0.201	0.363	0.718
life history pace	0.275	-0.028	0.547	0.071
brood size	0.038	-0.165	0.242	0.706
pre-treatment phase	-0.168	-0.446	0.098	0.231
treatment	-0.296	-0.674	0.057	0.147
treatment x pre-treatment phase	0.300	-0.084	0.686	0.129
treatment x duration of care	-0.358	-0.687	0.063	0.074
treatment x life history pace	-0.079	-0.398	0.301	0.657
duration of care x pre-treatment phase	0.143	-0.140	0.403	0.333
life history pace x pre-treatment phase	-0.033	-0.275	0.258	0.837
duration of care x pre-treatment phase x treatment	**0.434**	**0.020**	**0.783**	**0.031**
life history pace x pre-treatment phase x treatment	0.060	-0.335	0.424	0.761
random effects				
species	0.006	<0.001	0.013	
nest	0.280	0.099	0.472	
nestling	0.002	<0.001	0.018	
nest-phase	0.249	0.128	0.379	

Table S7. Mixed model results of effects on nestling mass gain during pre-treatment phase.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.002	-0.263	0.282	0.984
duration of care	0.160	-0.113	0.411	0.222
life history pace	0.177	-0.019	0.388	0.084
brood size	-0.031	-0.251	0.186	0.786
treatment	-0.007	-0.321	0.341	0.974
treatment x duration of care	0.076	-0.234	0.418	0.637
random effects				
species	0.005	<0.001	0.008	
nest	0.392	0.229	0.600	

Table S8. Mixed model results of effects on nestling mass gain during post-treatment phase.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.254	-0.104	0.581	0.139
duration of care	0.102	-0.249	0.404	0.525
life history pace	**0.319**	**0.059**	**0.600**	**0.029**
brood size	0.138	-0.135	0.428	0.339
treatment	-0.391	-0.841	0.007	0.067
treatment x duration of care	**-0.421**	**-0.854**	**0.022**	**0.037**
random effects				
species	0.023	<0.001	0.058	
nest	0.724	0.482	1.026	

Table S9. Full mixed model results of effects on nestling tarsus growth.

Effects	Estimate (β)	95% CI lower	95% CI upper	pMCMC
fixed effects				
intercept	-0.253	-0.550	0.031	0.082
duration of care	**-0.540**	**-0.818**	**-0.258**	**0.006**
life history pace	-0.036	-0.306	0.236	0.820
brood size	0.055	-0.111	0.233	0.543
pre-treatment phase	**0.559**	**0.159**	**0.927**	**0.004**
treatment	0.125	-0.229	0.487	0.494
treatment x pre-treatment phase	-0.373	-0.897	0.162	0.153
treatment x duration of care	-0.044	-0.390	0.294	0.822
treatment x life history pace	0.051	-0.316	0.383	0.792
duration of care x pre-treatment phase	-0.214	-0.568	0.139	0.247
life history pace x pre-treatment phase	0.345	-0.007	0.679	0.057
duration of care x pre-treatment phase x treatment	0.339	-0.191	0.787	0.163
life history pace x pre-treatment phase x treatment	-0.250	-0.786	0.214	0.327
random effects				
species	0.024	<0.001	0.101	
nest	0.001	<0.001	0.007	
nestling	<0.001	<0.001	0.001	
nest-phase	0.529	0.393	0.687	

Table S10. Selected mixed model results of effects on nestling tarsus growth.

Effects	Estimate (β)	95% CI lower	95% CI upper	pMCMC
fixed effects				
intercept	-0.265	-0.536	0.045	0.055
duration of care	**-0.577**	**-0.758**	**-0.430**	**0.004**
life history pace	0.093	-0.099	0.276	0.288
brood size	0.056	-0.109	0.230	0.514
pre-treatment phase	**0.592**	**0.260**	**0.939**	**<0.001**
treatment	0.120	-0.201	0.464	0.490
treatment x pre-treatment phase	-0.368	-0.907	0.058	0.112
random effects				
species	0.024	<0.001	0.129	
nest	<0.001	<0.001	<0.001	
nestling	<0.001	<0.001	<0.001	
nest-phase	0.523	0.396	0.667	

Table S11. Full mixed model results of effects on nestling wing growth.

Effects	Estimate (β)	95% CI lower	95% CI upper	pMCMC
fixed effects				
intercept	0.250	-0.159	0.644	0.157
duration of care	0.085	-.257	0.405	0.604
life history pace	0.118	-0.171	0.407	0.431
brood size	-0.041	-0.221	0.225	0.641
pre-treatment phase	**-0.402**	**-0.766**	**-0.040**	**0.041**
treatment	-0.113	-0.469	0.239	0.560
treatment x pre-treatment phase	0.038	-0.512	0.534	0.871
treatment x duration of care	0.304	-0.061	0.662	0.110
treatment x life history pace	-0.023	-0.391	0.323	0.876
duration of care x pre-treatment phase	0.256	-0.123	0.592	0.176
life history pace x pre-treatment phase	0.014	-0.348	0.396	0.959
duration of care x pre-treatment phase x treatment	-0.155	-0.660	0.330	0.535
life history pace x pre-treatment phase x treatment	0.060	-0.438	0.537	0.820
random effects				
species	0.061	<0.001	0.253	
nest	0.005	<0.001	0.038	
nestling	0.001	<0.001	0.005	
nest-phase	0.573	0.408	0.731	

Table S12. Selected mixed model results of effects on nestling wing length.

Effects	Estimate (β)	95% CI lower	95% CI upper	pMCMC
fixed effects				
intercept	0.290	-0.304	0.974	0.288
duration of care	0.073	-0.071	0.238	0.327
life history pace	0.110	-0.081	0.338	0.304
brood size	0.035	-0.246	0.282	0.774
pre-treatment phase	**-0.394**	**-0.779**	**-0.045**	**0.043**
treatment	-0.065	-0.401	0.289	0.706
treatment x pre-treatment phase	0.033	-0.480	0.580	0.910
random effects				
species	0.378	<0.001	1.22	
nest	0.003	<0.001	0.004	
nestling	0.001	<0.001	0.004	
nest-phase	0.565	0.405	0.712	

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Figures List

Tables List

Curriculum Vitae

PERSONAL INFORMATION

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EDUCATION

2010-2017 **PhD.** in Evolutionary Biology (Institute for Ecology and Evolution, University of Bern; Department of Anthropology, University of Zurich)

Subject: "Reproductive strategies and survival – relationship with ecology, social system and other life-history traits"

Supervision: Dr. Michael Griesser and Pr. Carel van Schaik

2007-2009 **Master of Science** in Biodiversity, Ecology and Evolution (University of Montpellier II)

Subject master project year 1 in island syndrome in birds: "Assessment of changes in morphology and secondary sexual traits of birds in island environments." (CNRS-Centre of Functional and Evolutionary Ecology, Montpelier, France)

Subject master project year 2 in conservation and behavioural ecology: "Analysis of spatial and social organisation of an endangered, urban population of long-nosed bandicoots (*Perameles nasuta*)." (UNSW Ecology and Evolution Research Centre of Sydney, Australia)

2006-2007 **Bachelor of Science** in Biology of Organism (University of Montpellier II)

2004-2006 **Higher National Diploma** (HND) in Biology speciality Biological and Biochemical analysis (University of La Rochelle)

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